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## BIOGEOGRAPHY OF THE BEES<sup>1, 2</sup>

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### ABSTRACT

Bees are most abundant and diverse in certain warm temperate, xeric regions of the world, especially the Mediterranean basin, the Californian region, and contiguous desertic areas. Other warm temperate xeric areas, like central Chile or the western part of southern Africa, have less rich faunas. Arid tropical regions, as well as tropical savannas, have poor bee faunas. For example, the southern margin of the Sahara and northern Australia are not rich in bees, in spite of the nearness of the former to the Mediterranean basin with past nondesert connections to the Mediterranean and the contiguity of the latter with the large warm temperate Australian faunal area. Equatorial savannas like those of east Africa are rather poor in bees.

Warm temperate, mesic areas, such as those of eastern North America, Europe, or the southern Brazilian to Argentina region of South America, also have rich faunas, although less so than do the Mediterranean basin and southwestern United States. Perhaps because of its small area, the climatically equivalent region in South Africa (largely in Natal) has a fauna that is best described as depauperate tropical, with certain temperate elements, but without great richness.

The moist tropics vary considerably in abundance and diversity of bees. In the Americas, they are almost or quite as rich as are the warm temperate mesic areas, but in Africa the fauna is far poorer, although richer than that of the Oriental region. There is a single Paleotropical bee fauna, richest in Africa and progressively smaller as one goes eastward across southern Asia to New Guinea, the Solomon Islands, and northeastern Australia. The poverty of the Oriental faunal region is shown by the number of genera and subgenera—89 compared to 175 in sub-Saharan Africa and 315 in the Neotropics (including temperate areas).

Thus unlike many groups which abound in the tropics, bees attain their greatest abundance in warm temperate areas. It is especially in such areas, principally xeric ones, that certain presumably archaic groups of bees have survived, and it is likely that various groups originated in such areas.

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The poor tropical African fauna as compared to the tropical American fauna may be due to the greater effects of past aridity in Africa (tropical savannas are poor bee habitats), and also to the inavailability of good faunas in nearby warm temperate areas. Southern Africa provides a much smaller source than the temperate South American area. The savanna (now desert) barrier isolating tropical Africa from the Mediterranean coast is much more developed than the xeric barrier isolating tropical America from temperate North America.

There is no close relationship between the number of species of bees in an area and the number of species of angiosperms. Thus the tropics with extremely rich floras have only moderate bee faunas. On a more local level, the same is true. For example, there is no extremely rich bee-faunal counterpart to the Cape flora of South Africa. On the other hand, floras and bee faunas are not independent of one another.

The percentage of oligolectic bees appears to vary with the number of species in flight at a given time. It is thus highest in the arid, warm temperate areas where climatic conditions lead to simultaneous flowering of many kinds of plants, hence simultaneous activity of many kinds of bees. Under such circumstances oligolecty should decrease competitive interactions among the bees; it should also increase pollinator effectiveness for the plants.

Specialist (oligolectic) bees must often be limited in distribution by the ranges of the plants from which they feed. However, plants are ordinarily not limited in distribution by the ranges of their oligolectic pollinators, for even obligate outcrossing plants apparently usually are adequately pollinated by generalist pollinators. Indeed some oligolectic bees have little or no significance as pollinators and are in effect parasites or predators on pollen.

Bees arose from sphecoid wasps after the appearance of probably beetle-pollinated primitive angiosperms. The place of origin is unknown but might have been the arid interior of west Gondwanaland (Africa, South America), an idea in accordance with the current abundance of bees in dry areas and the southern distribution of primitive groups of bees. The small bee faunas and lack of endemic archaic types on New Zealand and New Caledonia may indicate that there were no bees when this area separated from Gondwanaland before the middle of the upper Cretaceous. Distributions of archaic types in temperate parts of southern continents indicate an origin early enough for bees to have dispersed on the fragments of Gondwanaland, although narrow intercontinental seas may well have existed before such bee groups arose. The earliest fossil bees are Eocene, by which time there were already highly specialized long-tongued families. A moderate amount of time before the Eocene must have been necessary for the probably rapid initial radiation of the bees.

Bee faunas of oceanic islands indicate that minute bees are sometimes carried by winds for long distances, and that bees of all sizes that nest in wood or dead stems are also relatively likely to make major dispersal steps across water. Moderate sized and large ground nesting bees are less likely to jump major barriers, yet related species of such bees are found in New Zealand and Australia, indicating relatively recent dispersal across the water. In general, however, bees are rather sedentary and do not readily cross major barriers. Nonetheless many genera dispersed between North and South America before continental connections were established, no doubt inhabiting islands that existed between these continents during most of the Tertiary. The present Antillean fauna gives an idea of the groups of bees capable of such island-hopping. At least two large groups, the *Nomadinae* and the *Exomalopsini-Ancylini*, show evidence of an origin in South America and Tertiary spread probably via islands to North America, and thence to Eurasia.

Some major groups of bees (e.g., *Colletidae*, *Fideliidae*, *Exomalopsini*, *Nomadini*) appear from their distributions to have had their origins or at least major early evolutionary radiation in southern continents. Others (e.g., *Andreninae*, *Dufoureae*, probably *Halictini*) are equally attached to the Laurasian continents.

Most bee taxa have distributions which they could have attained with continents in their present positions, i.e., if they exist on more than one continent, they are on connected or nearby continents. This suggests that their dispersal has been relatively recent. Some taxa, however, show notable disjunctions, suggesting antiquity.

Some of the patterns of disjunction are as follows:

*a.* African-Oriental. Usually rather closely related tropical forms, probably isolated largely because of aridity of rather recent origin in southern Saudi Arabia, Iran, Pakistan, and northwestern India.

*b.* Western hemisphere amphitropical. Various taxa occur in temperate South America and also in North America, usually in the Sonoran and Chihuahuan regions, but not in the intervening tropics. Arid epochs combined with long distance dispersal must have been responsible

for such distributional patterns. There is some evidence that the north-to-south dispersal of amphitropical taxa was older than the south-to-north dispersal.

c. Asian-Australian. Few taxa, closely related in the two continents, suggest relatively recent dispersal; this route was opened by the approach of the continents and the appearance of intervening islands in the Miocene.

d. Xeric areas of North America, Central Asia, and South Africa (the *Hesperapis* group).

e. Largely xeric areas of Australia and North America, a few species in Central America and Colombia (*Hackeriapis-Chelostomoides*).

f. Pantropical in various combinations. The Meliponinae (several taxa) are the only pantropical bees (except for taxa that occur also in temperate areas). They have little ability to disperse across water gaps and since a modern genus occurred in the Eocene, the subfamily probably acquired its present distribution at least partly through the break-up of Gondwanaland. Some modern genera and subgenera must have existed in the uppermost Cretaceous.

g. Austral. The primitive family Colletidae is enormously better developed in temperate Australia than elsewhere. The tribe Paracolletini occurs not only in Australia but also in South Africa and temperate South America. The primitive family of long-tongued bees, Fideliidae, is limited to arid parts of southern Africa and Chile. These disjunctions may date to the end of the Cretaceous when water gaps among the southern continents were narrow, although cool temperate forms might have passed on land between South America and Australia via Antarctica as late as the end of the Eocene.

The time may seem premature for a paper on distributional history of bees in the sense that studies now under way on the cladistic relationships among bees will probably add to what can be said. In another sense, however, it is well to summarize our biogeographical knowledge of the group now, for biogeography is more than distributional history. Relations to climate and food resources (flowers), areas of abundance and diversity, means of dispersal, and the like are all related to biogeography and can be examined with or in part without detailed cladistic knowledge. Such information should be viewed with the cladistic findings, as they become known.

This paper consists of an examination of the distributions of major groups of bees (Hymenoptera, Apoidea), together with speculations as to the historical and ecological explanations of such distributions. Emphasis is placed on disjunct distributions, since they often shed special light on the historical factors involved.

Except for the section on relative abundance, for which numbers of species are used, the method is to examine the bees at the levels of genus and subgenus, usually without differentiating the two. (Thus if in a region there are three genera, one of them divided into four subgenera, I report six genera and subgenera for that area.) This procedure is used because different specialists, working with different groups and in different areas, have divided the bees differently; the groups regarded by some as subgenera are called genera by others. This problem does not disappear if one considers genera and subgenera as constituting a single classificatory level, but it is reduced. I have further reduced it by recognizing or not recognizing some groupings on the basis of personal knowledge and unpublished information. For the numbers of species reported in Table 1, I have sometimes made similar adjustments when synonymy or new species reported after a faunal study would considerably influence the figure given, or when it seems likely that subspecies will prove to be of specific status. The references in Table 1 are usually to the principal faunal studies; supplements except when very important are commonly not cited in order to avoid excessive expansion of the bibliography, but for Europe, the main area where supplements are a problem, most

are cited by Stoeckhert (1933). For areas where little revisional work has been done, I have sometimes used the number of species in a faunal list without adding any of the subsequently described species, thinking that synonymy will ultimately more or less balance the number of new species. Thus for Australia, while numerous new species of minute bees have been described since the major list of names was published in 1965, much synonymy remains to be recognized and published. Although the actual numerical data (numbers of genera and subgenera or of species) are somewhat shaky, relative numbers, whenever compared, have been evaluated and are believed to be good indices of the diversity at the genus-subgenus level in the areas or taxa being compared. The same applies to numbers of species, except that the unevaluated factor of intensity of collecting is even more important in this case.

The area of origin or of major radiation of a group cannot necessarily be recognized by its present area of greatest diversity or abundance. Nonetheless, in the materials below, I have frequently suggested that a taxon originated in or radiated in a certain continent or faunal area. Such speculation can be justified only when supported by other data, such as absence of the group in surrounding areas, and is always tentative, i.e., a hypothesis to be supported or rejected by other data.

#### AREAS OF DIVERSITY AND ABUNDANCE

For many groups of organisms, the tropics are the areas of maximum numbers of genera and species and of maximum morphological diversity. For this reason many groups are said to have originated in the equatorial regions, although the current restriction of tropical climates to those regions has not characterized climates through the evolutionary history of most major groups of organisms. Bees, however, appear to attain their greatest abundance, greatest numbers of species, and probably greatest numbers of genera and subgenera, not in the tropics, but in various warm temperate, xeric regions of the world (Michener, 1941, 1954; Linsley, 1958).

It is easy to make statements such as the above but to provide suitable documentation for them is difficult. The taxonomic literature is a poor guide because of our different levels of knowledge of different areas. In many parts of the world unnamed species are abundant. In some regions, like Africa, there are prodigious numbers of synonyms, mostly not yet recognized as such. One can better compare numbers of species taken in limited areas where bee specialists have worked for many years, because most of the species will be recognized, even if not properly identified, in such a study. A problem is that such areas differ in size and local vegetational, edaphic, and topographic diversity, and the bee specialists differ in the vigor with which they have sought to survey their local faunas. Thus differences in the faunas as published may result in part from factors other than genuine faunal differences. Similar problems exist if one compares faunal lists for larger areas—states, countries, etc. The data given below, however, give some idea of the number of species in certain regions. The greatest problem is scarcity of data outside of the Palearctic and Nearctic regions, so that claims of relatively poor tropical faunas are not abundantly substantiated. In my own experience collecting bees in tropical areas, however, I have been impressed

by the relative scarcity of bees (individuals and species) compared to their abundance in xeric, warm temperate regions. (The richest tropical areas are those of the Americas, and are a possible exception to this statement in terms of numbers of species.)

Table 1 lists some of the faunal studies that have been made, arranged by biogeographical areas. More or less continent-wide lists or catalogues have not been included (except for Australia), since they cover areas of such size and climatic diversity that they contribute nothing to the recognition of centers of abundance and faunal diversity.

The bee fauna is particularly rich in the Mediterranean basin and thence eastward to central Asia, and in the Madrean region of North America (=Californian and the desertic regions of the southwestern United States and northern Mexico). This richness is only indicated vaguely for the Palearctic region in Table 1, for there are no adequate studies of local faunas in the areas concerned. The large fauna of Spain (1,043 species recorded by Cebellos, 1956, without very detailed collecting or intensive studies) suggests such richness, but Spain includes diverse areas, high montane habitats to Mediterranean macchia, so that some Spanish species are boreal or mid-European rather than Mediterranean. The large fauna of southwestern France (491 species recorded by Pérez, 1890) is also indicative of the rich Mediterranean bee fauna. Local faunas in the Mediterranean area may contain over 300 species, and with careful collecting the number might in some places exceed 400 (see Graeffe, 1902, for the Trieste area).

For the equivalent Nearctic region, the Madrean, the enormous bee fauna of California is impressive, but California includes even more climatic zones than Spain. Part of the large size of the Californian fauna is due to the large area, north-south extent, and altitudinal and precipitational range found within the state. In the chaparral or macchia region, i.e., the area having a Mediterranean climate, however, the fauna is large, as shown by 439 species from the vicinity (within 16.6 km = 10 miles) of Riverside. Palm Springs, on the interface between such an area and the Sonoran desert, has an even larger bee fauna (probably about 500 species) thanks in part to local topographic and vegetational diversity.

Eastward through desert and arid steppe, from the Mediterranean Basin to central Asia, and from the Californian region to Texas, faunas are also rich. There are few faunal reports in these areas, but data do exist for some outlying regions. Northern and more humid prairie and steppe regions like North Dakota have only moderate-sized bee faunas. Popov's (1967a) report of 305 species from central Asia is probably rather incomplete; Pesenko's (1971-1975) 347 species from the Lower Don is probably more complete. The large lists of species from New Mexico and Wyoming (both assembled without detailed collecting, although that from Wyoming includes species from neighboring states) indicate rich bee faunas.

Moldenke (1976a, 1976b) has compared the bee faunas of various vegetational areas in California and the Pacific northwest. He finds the chaparral or macchia areas and the sparse forests of the southern mountains, i.e., the Californian areas of Mediterranean climate, richest in bee species, the Californian deserts (north-

TABLE 1. Some faunal studies of bees, indicating the number of species reported for various areas.

<i>A. Palearctic Region</i>	
Spain (Cebellos, 1956)	1,043
France (Gaulle, 1908)	769
Britain (Saunders, 1896; Richards, 1937)	240
Holland (Benno, 1969)	328
Switzerland (Frey-Gessner, 1899-1912)	458
Denmark (Jørgensen, 1921)	217
Germany (Stoeckert, 1954)	566
Hungary (Friese, 1893a)	505
European USSR (Osychnyuk et al., 1978)	950
Finland (Elving, 1968)	230
Ireland (Stelfox, 1927)	80
Iceland (Petersen, 1956)	1
<i>Regional and Local Lists</i>	
Arctic Norway (Sparre-Schneider, 1909)	26
Bedfordshire, England (Chambers, 1949)	159
Devon, England (Perkins, in Stelfox, 1927)	181
Southwestern France (Pérez, 1890)	491
Nord & neighboring regions, France (Cavro, 1950)	327
Saone-et-Loire, France (Marchal, 1893)	141
Haute-Marne, France (Frionnet, 1905)	155
Suisse Romande (Beaumont, 1960)	114
Parc National Suisse (Beaumont, 1958)	201
Neuchâtel, Switzerland (Beaumont, 1955)	261
Northwest Germany (Stoeckert, 1933)	263
Köln (= Cologne) (Aerts, 1949)	266
Mangfall region (Brassler, 1959)	366
Franken (Stoeckert, 1933, 1954)	443
Amrum Island (Haeseler, 1976)	64
Bremen (Alfken, 1939)	288
Baden (Strohm, 1924; Stoeckert, 1933)	399
Nassau (Buddeberg, 1895; Wolf, 1955)	348
Sachsen (Krieger, 1894; Stoeckert, 1933)	340
Mecklenburg (Friese, 1893b; Tiede, 1917)	238
Brandenburg (Schirmer, 1911; Stoeckert, 1933)	329
Thüringen (Rapp, 1945)	390
N. W. Thüringen (Blüthgen, 1916)	219
Pommern (Blüthgen, 1919, 1942)	273
Ostpreussen (= East Prussia) (Alfken, 1912a)	240
Westpreussen (= West Prussia) (Alfken, 1912b)	294
Schlesien (Ducke, 1898, 1900; Stoeckert, 1933)	347
Prov. Poznan (= Posen) (Torka, 1913; Stoeckert, 1933)	276
Poznan (Banaszak, 1973)	132
Puniny Natl. Park, Poland (Dylewska, 1962; Dylewska & Noskiewicz, 1963)	173
Tirol, Austria (Schletterer, 1887)	372
Dept. Zemplén, Hungary (Chyzer, 1886)	253
Trieste coastal region (Graeffe, 1902)	366
Trieste, Italy (Graeffe, 1890, 1895)	269
Southwest provinces of Finland (Valkeila, 1962)	195
Ukrainian Carpathians (Osychnyuk, 1967)	172
Bashkirskaja ASSR (Nikiforuk, 1957)	331
Steppes of Lower Don, USSR (Pesenko, 1971-1975)	347
Central Asia (Popov, 1967a)	305
Obihiro, Hokkaido, Japan (Usui et al., 1976)	82
Minami, Gifu Prefecture, Japan (Yamauchi et al., 1974)	57
Bonin Islands (Yasumatsu, 1955)	8

TABLE 1. Continued.

<b>B. Nearctic Region</b>	
California (Moldenke & Neff, 1974)	1,985 <sup>a</sup>
New Mexico (Cockerell, 1906)	551
Wyoming (Lavigne & Tepedino, 1976)	663
Eastern USA (Mitchell, 1960, 1962)	859
North Dakota (Stevens, 1949-1952)	244
Michigan (Mitchell, 1960, 1962)	403
North Carolina (Mitchell, 1960, 1962)	521
<i>Regional and Local Lists</i>	
Northern Ellesmere Island (Richards, 1973)	2
Riverside, Calif. (P. H. Timberlake, in litt., 1950; Linsley, 1958)	439
Palm Springs, Calif. (P. H. Timberlake, in litt., 1950)	±500
Boulder County, Colo. (Cockerell, 1907)	186
Western Wisconsin (Graenicher, 1935)	184
Eastern Wisconsin (Graenicher, 1935)	217
Chicago region (Pearson, 1933)	169
Carlinville, Illinois (Robertson, 1929a)	297
Hattiesburg, Miss. (Michener, 1947)	103
Miami, Florida (Graenicher, 1930)	64
<b>C. Oriental Region</b>	
Java (Friese, 1914; M. A. Lieftinck, in litt.)	193
Philippines (Baltazar, 1966)	233
Micronesia (Krombein, 1950)	26
Solomon Islands (Krombein, 1951)	24
Fiji (Fullaway, 1957)	8
Samoa (Perkins & Cheesman, 1928)	13
Hawaiian Islands (Perkins & Forel, 1899)	54
<i>Local List</i>	
Barrackpore, Bengal (Rothney, 1903)	73
<b>D. Australian Region</b>	
Australia (Michener, 1965a)	1,618
<b>E. Neotropical Region</b>	
Costa Rica (Friese, 1916, 1921, 1925)	230
Panama (Michener, 1954)	353
Cuba (Alayo Dolmau, 1973)	107
Surinam (F. N. Dingemans-Bakels, in litt.)	293
<i>Regional and Local Lists</i>	
Barro Colorado Island, Panama Canal Zone (Schwarz, 1934a, 1934b)	76
St. Vincent & Grenada (Ashmead, 1900)	36
Belém, Brazil (Ducke, 1906)	251
Paraná, Brazil (3 localities) (Laroca, 1974)	255
Mendoza, Argentina (Jørgensen, 1912)	230
Desertic parts of Chile (Moldenke, 1976b)	176
Mediterranean climatic areas of Chile (Moldenke, 1976b)	183

<sup>a</sup> Moldenke & Neff (1974) actually list 2,042 species and subspecies. I have omitted a few extralimital ones and some subspecies that are unlikely to be recognized later as species. However, Moldenke (1976a) on different pages gives the number of species of bees in California as "1,000+" and as 1,200, without explaining the major difference from the earlier work in which the species were listed by name. In another paper (1976b) he gives the total number of bee species in the Pacific slope from Baja California to southern Alaska as 1,974.

western part of the Sonoran region) nearly as rich, and the boreal forests, grasslands, and the coastal zone progressively poorer. The actual numbers of species vary greatly according to how he divides the area, but representative numbers are 676 for the southern chaparral areas, 668 for the deserts, 589 for the mountain forests of California, thence diminishing to 129 for the coastal strip.

Other xeric warm temperate areas such as central Chile and Argentina, much of Australia, and western parts of southern Africa also possess large bee faunas, although to judge by the taxonomic literature and collecting impressions, they are smaller than those cited in the preceding paragraphs. Unfortunately there are few faunal data for these areas. There is a species list for Mendoza, Argentina (Jørgensen, 1912), as shown in Table 1. Moldenke (1976b) has compared the faunas of the temperate coastal areas of Chile and the western United States. For the climatically Mediterranean area of Chile and for the deserts he reports 183 and 176 species respectively, while comparable figures for California are 676 (for the southern part of the Californian Mediterranean area only) and 668 (for the Californian deserts). The full meaning of these numbers is not clear, in part because of the problem indicated in the footnote to Table 1, and in part because of the less intense collecting in Chile than in California. Moldenke, however, believes the differences in number of species between comparable Californian and Chilean areas to be real, and I see no reason to disagree with him.

In mesic temperate areas such as the eastern United States or central Europe, the numbers of individuals and species are markedly less than in the xeric regions of the same continents. Local lists generally have fewer than 300 species, exceptions mostly being those for more southern localities or large areas. One of the most carefully collected localities in the world must be Carlinville, Illinois, where Robertson found 297 species. The large number of species (566) reported for Germany might cause one to question the view that central Europe has a smaller fauna than that of the Mediterranean, but it must be remembered that Germany is a moderately large and diverse area that has been meticulously collected in many localities by a large number of specialist collectors of bees. Such careful collecting has never been done in any Mediterranean area.

As indicated in Table 1, bee faunas decrease rapidly as one approaches and enters the Arctic, in spite of the abundance of flowers in arctic habitats.

The few data from the tropics in Table 1 appear to support the view that tropical bee faunas are not as large as those of some temperate xeric and mesic areas. The local fauna of Barrackpore in Bengal was sampled by a person interested in bees and wasps over several years and yielded only 73 species. There is no way to judge the intensity of the collecting, however. The fauna of Java, about 193 species, should be viewed in the perspective that it has been studied by persons having special interests in bees and that Java is a large, altitudinally diverse island that was connected with Asia so recently that it has a rich Oriental fauna, not a specialized insular fauna.

My impressions of the African tropics, in the absence of appropriate data, are that the bee fauna is richer than that of the Oriental tropics. The American tropics are richer still. Thus Panama has a smaller area than Java, but a much larger known bee fauna, and certainly many species yet to be discovered. Indeed the



the vicinity of Belém do Pará, Brazil, a low, flat region, has a much larger fauna than the whole of Java with all of its diversity. My own observations, supported strongly by those of Dr. J. van der Vecht (in litt.) who has worked both in Indonesia and Surinam, are that flowers attractive to bees are far more abundant and diverse in and at the edges of forests in the Neotropical than in the Paleotropical regions. Presumably the bees and flowers coevolved. It is not clear why such a regional difference should exist. The important point is that, although data from the tropics are meager, Table 1 and collecting impressions both clearly show that there is no great abundance of species (or genera) in the tropics as compared to temperate regions.

There are various possible explanations for the abundance of bees in some xeric areas and their scarcity, relative to what would be expected from experience with other organisms, in the tropics. Most bees, like the sphecoid wasps, store their highly perishable larval food (for bees, pollen mixed with nectar) in cells excavated in the soil and only thinly lined with secreted waxy or cellophanelike material. In humid environments the loss from fungal attacks on such food and on immature bees is substantial and sometimes catastrophic. Dr. J. G. Rozen has suggested (in litt.) that another problem for bees in humid areas may be hygroscopic liquification of the food provided for their larvae, which therefore drown. As noted below, the bee groups that are most successful in humid areas are mostly those of that no longer nest in the soil, or that do not use simple cells excavated in it. An unusual case of larvae in excavated cells in the tropics surviving for months below the water table is that of *Epicharis zonata* which lines and seals its cells with thick resinous material (Roubik & Michener, in press). Even larvae in the rather simple cells of Andrenidae and Halictidae may survive flooding for a few days (Michener, personal observations). Nonetheless, most bees do not live under such conditions and the disjunct southern distribution of certain primitive groups of bees, as described in the subsequent sections, is consistent with an origin of bees in xeric parts of Gondwanaland.

Another reason for the moderate size of the bee faunas in the humid tropics may be the success of a few kinds of highly social bees there, as suggested by D. W. Roubik (in litt.). The genus *Apis* is represented by three of four species in southeast Asia, one species in Africa, and was until recently absent in the Americas, while the other highly social bees (Meliponinae) are most abundant in the Americas. Each such species may be, from the standpoint of floral resources, the ecological equivalent of a number of species of nonsocial bees, for the highly social species are active all year and are generalists while the nonsocial species are often seasonal. Indeed, it is possible that each of the highly polylectic *Apis* species is the equivalent of several meliponines and many solitary species. Competition from aggressive generalists could have an important influence on the tropical faunas.

Table 2 summarizes, in part subjectively, the relative abundance and diversity of bees in various climatic and geographical areas. Of course, much depends on the particular areas compared, for the local soil, floral conditions, temperature, and other factors play a major role.

It seems that some of the world's warm temperate, xeric areas are, for bees,

TABLE 2. Relative abundance and diversity of bees in various areas, from most abundant (1) to least abundant (10).

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1. Warm temperate xeric (Mediterranean, Mediterranean to Central Asia)
  2. Temperate mesic
  3. Moist tropical (American)
  4. Other warm temperate xeric areas (S. Africa, Australia, Chile, etc.)
  5. Temperate prairie, steppe
  6. Moist tropical (Old World)
  7. Tropical grasslands and savanna
  8. Cool temperate xeric
  9. Extreme deserts
  10. Frigid areas
- 

what the tropics are for many other groups. That is, these areas are centers of diversity, of evolution, perhaps areas of origin for various taxa, and reservoirs for taxa which have never extended more widely or have retreated to and survived in these xeric areas. A problem with this concept is that the dry areas of the world are not necessarily ancient. For example, those of North and South America probably date only to the Pliocene. As will be suggested below, bees very likely arose in dry areas and have radiated to a major degree in such areas. Groups actually restricted to them probably spread by long distance dispersal. (Shorter distances sufficed in dry epochs or between edaphically dry areas.) Moreover, mesic-adapted taxa probably entered and proliferated in dry zones. Thus when a dry region arose, it could be populated by a bee fauna that often became larger than that of adjacent mesic regions.

Mere aridity, however, does not assure a large bee fauna. Mediterranean climates (winter wet season, warm dry summers, macchia or chaparral vegetation) have rich faunas, as exemplified by parts of California and the Mediterranean basin. So also do still more xeric warm regions with regular but small rainfall, characterized by extensive development of succulent vegetation such as cacti, African *Euphorbia*, and Aizoaceae. Thus the desertic region (Sonoran and Chihuahuan) of the southwestern United States and northern Mexico has a large bee fauna, both in those parts (west of about 113° W) where the rainfall is principally in winter and in those where it is in summer. The contrast is striking with areas in the same latitude but with a mesic climate, such as the eastern United States. Cool desertic areas, like the northern part of the Great Basin of North America or much of Patagonia, also do not have especially large bee faunas.

Interestingly enough, the contrast is also striking with tropical and subtropical xeric areas. For example, there is no evidence of an enriched bee fauna along the southern edge of the Sahara, in spite of the proximity of a very rich Mediterranean fauna in North Africa, and in spite of climatically habitable areas that must have joined these zones in various places in relatively recent, more humid times. Also, there is no evidence of faunal richness compared to nearby areas in several other dry regions in or near the tropical zone. Thus northeastern Brazil, northern Australia, northwestern India and western Pakistan, so far as known, have poor faunas compared to other parts of the same continents. Tropical savannas such as those of east Africa, Venezuela, Panama (Michener, 1954), and northern Queensland also have poor faunas, and the drier tropical areas are in

effect depauperate savannas. To the bee collector, arid tropical areas appear to have much less flowering throughout the year and less synchronization of flowering than the warm temperate, dry areas.

Warm temperate grasslands (prairie or steppe), especially the more mesic or cooler ones, have moderate bee faunas, becoming rich where the grasslands are arid and interspersed with xeric vegetation like that of the Sonoran and Chihuahuan deserts. Bee faunas of temperate grasslands are substantially larger than are those of tropical grasslands and savannas. Prairies have conspicuous flowering seasons with many kinds of flowers, in contrast to many tropical savannas. In South America there is more or less continuous savanna and grassland from central Brazil to the Argentina pampa, with the bee fauna seeming to become richer as one progresses southward, and probably becoming richer still in the desertic parts of central Argentina, which resemble the Sonoran region in vegetational aspect.

There are, of course, certain groups of bees that are not most abundant and diversified in the xeric warm temperate areas. The principal such groups are the following:

**Hylaeinae:** Most abundant and diversified in mesic or humid areas, temperate and tropical. Scarce in desertic areas, perhaps because of scarcity of pithy stems which are the favored nesting sites.

**Ceratinini:** The same comments apply except that this tribe is not much diversified in the temperate areas of the Northern Hemisphere.

**American Halictinae:** Most common in temperate and tropical mesic or even humid areas, usually scarce in xeric areas except in limited mesic environments therein. In the Palearctic region, however, various halictines (e.g., *Halictus* s. str., *Vestitohalictus*, *Nomioides*) are abundant, with many species in Mediterranean and similar climates.

**Andreninae, Macropodinae, the genus *Nomada*, Bombini:** Most common in mesic temperate, even cool temperate, areas; distinctly less common or almost absent in desertic as well as tropical regions.

**Nomiinae, Ctenoplectrinae, Xylocopini, Tetrapediini, Centridini, Ctenioscheolini, Rathymini, Meliponinae, Apinae, Euglossini:** Best developed in tropical, mostly moist tropical, habitats. These groups (except Nomiinae) occur commonly in forested regions and mostly nest in wood, in preformed cavities of various sorts, in termite nests, or line their cells with resin or wax (Centridini) or are parasites in nests of Centridini. Thus except for Nomiinae and some Centridini, they do not construct nests in soil like most solitary bees and are therefore presumably less subject than most to damage to food and immature stages by moisture and fungi. [Several other groups (e.g., Augochlorini among American Halictinae; Exomalopsini) have many genera and species in moist tropical regions even though they are most abundant outside of such areas.]

Most groups of bees other than those listed above are either as abundant and diversified in warm temperate xeric areas as elsewhere, or are more so. More details, together with bibliographic references, are given in the section on DISTRIBUTIONS OF THE GROUPS OF BEES.

## ORIGIN AND ANTIQUITY OF BEES

There is no doubt, on morphological grounds, that bees arose from the sphecoid wasps. There is no evidence that any extant sphecoid group is most closely related to bees, or is ancestral to them; the bees and sphecoid wasps probably had a common ancestor that had wasplike feeding habits and that would be considered a sphecoid wasp if it were known to us. It is clear that a shift from animal food to pollen as the principal protein source was the major event in the origin of bees. Indeed, the bees are probably best regarded as a part of the Sphecoidea rather than as a separate group of the Hymenoptera (Brothers, 1975).

All bees are dependent on products of angiosperm flowers (nectar, pollen, sometimes oil) for food. The group therefore must have arisen at the same time as or after the angiosperms. Various authors (e.g., Baker & Hurd, 1968) have noted that the more primitive groups of angiosperms (e.g., Magnoliaceae) are largely pollinated by beetles. Hence it seems likely that bees arose or at least became common with the subsequent evolution of angiosperms. In their excellent review of angiosperm biogeography, Raven & Axelrod (1974) indicate that angiosperm fossils first appear in middle Lower Cretaceous, that by early Upper Cretaceous angiosperm pollen is becoming more abundant than spores of ferns and pollen of gymnosperms, and that by the end of the Cretaceous there was much diversity among angiosperms. Some forms present at that time (e.g., Myrtaceae, *Ilex*) are in families and genera now visited extensively by bees, and it is probable that bees were present and perhaps abundant by that time (Maastrichtian, 65–70 m.y. BP).

The earliest known fossil bees are from the late Eocene Baltic amber (see review by Zeuner & Manning, 1976, and for Meliponinae, by Wille, 1977). That fauna includes diverse groups of bees, including long-tongued families, especially the Apidae. It is obvious that the bees had already evolved for some time before the late Eocene.

It is probable that bees arose in the Upper Cretaceous. The complete absence of unusual archaic bees from New Zealand and New Caledonia, however, might suggest that there were few or no bees in Gondwanaland when these areas were isolated 60 to 80 m.y. BP (Smith & Briden, 1977), after the middle of the Upper Cretaceous, by the splitting of that continent. A more likely explanation is that bees were scarce in the moist temperate forests of these islands and eastern Australia when the split occurred (Raven & Axelrod, 1972); they may have been better represented in other places and any that were on these islands may have been exterminated during the long subsequent history of changing climates and sea levels.

Except for fossils in amber, wings are often the only well-preserved fossil structures. Unfortunately, while wings often contain many useful characters, they may not indicate the family to which a bee belongs. Relations of species not assignable to modern genera are therefore highly suspect, especially when published by persons who were not bee specialists. The following list indicates the earliest records that, from the literature, seem probably accurate, for various groups of bees:

- Halictinae—Oligocene (Colorado)  
 Andreninae (*Andrena*)—Eocene (Baltic Amber)  
 ?Ctenoplectrinae—Eocene (Baltic Amber)  
 Melittinae (*Melitta*)—Oligocene (Colorado)  
 Anthidiini—Oligocene (Colorado)  
 Megachilini—Oligocene (Colorado)  
 Xylocopini—Miocene (perhaps Oligocene) (Europe)  
 Anthophorini—Oligocene (Colorado)  
 Meliponinae—Eocene (Baltic Amber)  
 Bombini—Oligocene (Colorado)  
 Apini  
   (*Electrapis*)—Eocene (Baltic Amber)  
   (*Apis*)—Oligocene (Europe)

Speculations as to antiquity of various groups, based on distributional considerations, will be included in subsequent sections. The only use for the above list is to indicate minimum ages of groups. Not a single fossil bee (except some Pleistocene or Recent *Trigona* assigned to extant species) has been found in the southern continents. The fossil record, in short, is so poor as to have almost no biogeographical significance (except in the genus *Trigona*).

The presence of long-tongued Apidae (forms with mouthparts much modified as compared to wasps) in the Eocene suggests rapid early radiation. It is likely that most bee families were recognizable in the Eocene and quite possibly before. One of the problems in understanding bee evolution is how so much of the evolution of the group could have occurred in the perhaps 20 to 30 m.y. from the appearance of probably bee-pollinated plants (taxa now visited by bees) in the latest Cretaceous (Maastrichtian) until the Eocene when fossils show the presence of the presumably most derived family, Apidae. Major morphological reorganizations, particularly of the mouthparts, are involved. As will be noted in subsequent sections, biogeographic evidence suggests an earlier origin for bees than the Maastrichtian. Much of the reliable evidence of times of appearance of angiosperm groups is based on fossil pollens (Muller, 1970). Before late Cretaceous, most of the pollen is unidentifiable as belonging to any modern group of plants. It is therefore likely that early bees utilized some of these pollens and that one need not delay the origin of bees until appearance of known bee-pollinated plants. Such plants, moreover, tend to produce limited quantities of sticky pollen that does not blow extensively in the wind. It may be, therefore, that bee-pollinated plants became abundant, especially in dry areas, well before their pollens appeared in the fossil record. For those reasons one can postulate that bees arose earlier, let us say, by mid-Cretaceous. This would have allowed them 60 m.y. of evolution before their first fossil appearance and their early radiation could have been relatively gradual.

The place of origin of bees remains obscure but one can speculate both as to the place and its climate. The xeric interior of the old continent of Gondwanaland, particularly West Gondwanaland (Africa-South America), has been suggested as the area of origin of angiosperms (Raven & Axelrod, 1974). It presum-

ably had a seasonal temperate climate. Xeric regions, especially those with sandy soils, are commonly areas of abundance for sphecoid wasps, most of which nest in the ground. It is not unlikely that bees arose from these wasps in such a place. If so, they have retained their association with xeric areas and have been, compared to the angiosperms, relatively unsuccessful in adapting to humid climates. Possible reasons for this have been discussed previously in the section on AREAS OF DIVERSITY AND ABUNDANCE.

#### DISPERSAL OF BEES

Because bees fly well, one might think that they would be rather successful at crossing barriers, such as water or areas that are climatically or vegetationally inhospitable. A female bee usually mates early in adult life and carries enough sperm cells alive in her spermatheca to last for part or all of her reproductive life. One can therefore assume that, except for the few highly social bees (Meliponinae, Apinae) that must swarm as a communicating group to establish new colonies, an individual female transported across a barrier might be able to nest, reproduce, and thus establish a population. If she carried sperm from several males, as is likely for many species, the genetic limitations of such a new population would not be so severe as if she had mated only once. The ability of a bee in a new area to fly about and perhaps find suitable nest sites and food sources also would seem to enhance the probability of establishment.

Nonetheless, distributional data suggest that most groups of bees are not particularly good at crossing major barriers. Most bees fly only in good weather so that they are likely to be in their nests during storm winds. Moreover, not only individuals but successive generations of solitary to primitively social species commonly return to the same nesting site, so that they tend to be quite sedentary (Michener, 1974).

Michener (1953) noted, for *Megachile brevis*, that when favored flowers in an area wilted, bees left, and appeared and continued nesting in other areas. One marked female appeared 8.8 km from the site where it had been nesting. Moreover, E. G. Linsley (in litt.), discussing the spotty blooming of desert flowers in response to spotty rainfall, notes that in 1959 large numbers of females of *Andrena linsleyi* dug burrows near a small patch of the host flower, *Oenothera deltoides*, most of the bees, perhaps, having migrated from surrounding sites now with few flowers but where the *Oenothera* bloomed profusely in the two preceding years. The nearest such site was 3.2 km distant. Such dispersal is unusual, however. For most solitary or primitively social bees, while some individuals must disperse, and of course new nesting sites do develop, the majority of individuals seem to remain at established sites. If conditions are bad, the population diminishes, seemingly not because of dispersal but because of death or failure to reproduce.

Thus for the majority of kinds of bees, dispersal has been by slow spread across continents or to nearby land masses, or by transport on moving continents. The Antillean and central Indonesian faunas, however, show that scattered islands between continents can serve as stepping stones for many taxa.

There is some evidence that solitary to primitively social bees that nest in wood

or stems are more likely to cross moderate water gaps than are those that nest in the ground. Thus a large percentage of the long-tongued (relatively derived) genera of bees in Australia belong to groups such as Lithurginae, Megachilini, and Xylocopinae that commonly nest in stems or wood (Michener, 1965a). The same groups are a major part (although by no means the only components) of the Indo-Australian tropical fauna that extends from India to Southeast Asia, Indonesia, and in diminishing numbers to the Solomon Islands and northern Australia. Many water gaps existed in this region even in times of lowered sea levels, yet some species are very wide ranging in it, showing repeated, relatively recent, successful crossing of water. Perhaps wood or stems are rafted or blown in severe storms often enough to account for the higher frequency of such distributions in these bees than in ground-nesting forms.

When one examines the bee faunas of oceanic islands, it becomes apparent that dispersal across water favors minute forms in addition to the moderate-sized to large, wood-nesting species. For example, on the oceanic islands of the Pacific (Fiji, Samoa, Hawaii, Micronesia, etc.) there are a few moderate-sized, wood-nesting *Lithurge* and *Megachile*, perhaps carried to some of the islands by Polynesians. Otherwise the fauna consists largely of small ground-nesting *Homalictus* (Halictini) or of *Hylaeus*; the latter are also small bees but they nest in wood, in stems, or in holes in rocks or soil. It is only among the small forms, especially *Hylaeus* in Hawaii (Perkins & Forel, 1899) and *Homalictus-Echthralictus* in Samoa (Michener, 1978a), that there has been significant evolution in these isolated oceanic islands. Thus it seems that dispersal, presumably by wind at least for *Homalictus*, must have favored small forms, while the larger ones probably came later and perhaps in some cases with the help of man. The New Zealand fauna, however, consists largely of middle-sized ground-nesting *Leioproctus* from Australia, and the Galapagos Islands lack small bees and have only one large form, the wood-nesting *Xylocopa darwini*, which belongs to a tropical American subgenus. The presence on the Galapagos of the large meloid parasite (*Cissites*) of *Xylocopa* suggests arrival of the bee from the mainland in a floating log (E. G. Linsley, in litt.) although the female bees are powerful fliers and have been seen far out to sea among the islands (Linsley, in litt.; Cheesman, 1929).

Less isolated island groups frequently have larger faunas, including small as well as larger bees, both those that nest in soil and those that nest in wood. For example, the rather large megachilid *Creightoniella frontalis* (and its subspecies or allied species *C. atrata*) ranges for 6,400 km from Sumatra to the Solomon Islands; this is a ground-nesting species, and presumably the adults have flown or been blown across the water gaps. The Antillean fauna has probably all or nearly all arrived across the water. Yet it includes not only bees that nest in wood and minute bees, but also moderate-sized to large ground-nesting bees such as *Caupolicana*, *Melissodes*, *Anthophora*, *Agapostemon*, etc. (Alayo Dolmau, 1973). They probably were blown from Yucatán or elsewhere by hurricanes or other storms.

The highly social bees (Meliponinae, Apinae) present special biogeographical problems. They disperse by swarming or by absconding as colonies, not by individuals, most of which in any case are nonreproductive workers. In Meliponinae, a new colony is established by individuals from the parent colony which go

back and forth provisioning the new nest, before a queen goes there. Thus dispersal by flight across even a few hundred meters of water would be impossible, a view supported by the apparent isolation of some species or subspecies by Brazilian rivers (J. S. Moure, verbal communication). The absence of Meliponinae from the Antilles (except for one species probably introduced by primitive man), in spite of their abundance on the mainland, supports this view, although there is a fossil *Trigona* from Hispaniola. The presence of Meliponinae through the East Indies and as far east as the Solomon Islands, however, suggests other means of dispersal. In Apinae dispersal is by swarms or migrating colonies which may fly for distances of perhaps dozens of kilometers, or across habitable country where they can stop, hundreds of kilometers. Yet traversal of a broad ocean by an organized swarm would be impossible. There are three mainland *Apis* species in the Philippines, but the water gaps were much narrower or absent when the sea level was lowered in the glacial periods.

In view of the distribution of Meliponinae in the East Indies, these bees must rarely cross substantial water barriers as colonies in natural rafts or perhaps even in hollow logs floating in the sea. They store food supplies, and those that inhabit hollow logs often close entrances with waterproof resin under unfavorable conditions, and therefore might survive weeks of drifting. Nests of *Melipona compressipes manaosensis* in the Amazonian riparian forests survive long annual periods of submergence in river waters (Kerr, 1969). The presence of *Apis* east of Wallace's Line in Indonesia (*A. dorsata* as far east as Timor) may be explained similarly. However, migrating swarms of *Apis* may occasionally cross water gaps like those among the Indonesian islands, or at least the narrower ones of the glacial periods.

#### FLORAL RELATIONSHIP

This section is not a comprehensive treatment of floral relationships of bees. It concerns only those topics having direct relationship to geographical distribution, and cites only certain examples, among many that are known, of the relationships described.

Bees vary widely in their floral requirements. Most will take nectar from a variety of kinds of flowers. Hence male bees and females that are not collecting pollen are not usually very specific in their flower visiting habits. Some species likewise collect pollen from many different and unrelated kinds of flowers. Such bees are called *broadly polylectic* (supergeneralists of Moldenke, 1975). Other species restrict pollen collecting to a few related flowers, commonly in the same genus (or even to a single species) and are called *oligolectic* (or *monolectic*). These are the superspecialists of Moldenke (1975). Presumably the majority of bees collect pollen from several kinds of flowers (not necessarily closely related) in most of the communities that they inhabit, often from different flowers in different communities or at different seasons. Such forms are called oligolectic by Moldenke (1975) but this is contrary to the usual use of the word. The expression *narrowly polylectic* seems in accordance with common usage for such forms. All intergradations exist between broadly polylectic species (such as *Apis melli-*



*fera*) and oligolectic or monolectic species. The distinction that is most often confusing is between oligolectic and narrowly polylectic, and there will always be differences of opinion for some species. However, if a bee collects pollen only or very largely from a few related species of a genus or family of plants, it is oligolectic, whereas if it collects from unrelated plants (e.g., like some *Osmia* of the subgenus *Nothosmia*, from *Phacelia*, Hydrophyllaceae; certain species of *Penstemon*, Scrophulariaceae; and perhaps a few Leguminosae), I would call it narrowly polylectic, even if only a few floral species are involved. This usage is in accordance with that of Robertson (1899), Malyshev (1936), and others, often using the root—trophic rather than—lectic. There is no need to discuss here the morphological interrelations that sometimes are obvious between oligolectic bees and their favored flowers, nor the attributes of the flowers visited by a bee species that utilizes several kind of flowers. In the present context, the important point is to determine the possible influence of the distributions and abundance of flowers on the distributions of bees.

Obviously bee faunas and the floras of flowering plants with which they are associated are interdependent. Yet there is no close relationship between the numbers of species in each. Thus the moderate-sized floras of the Galapagos Islands and Iceland are associated with only a single polylectic bee species each, *Xylocopa darwini* on the Galapagos and *Bombus jonellus* on Iceland. Moreover, the very rich tropical floras are associated with only moderate-sized bee faunas. The same inconsistencies are found on more local levels. For example, the extraordinarily rich flora of the Cape region of South Africa is associated with a moderate-sized bee fauna, and it is my impression from collecting experiences that as one goes inland from the Cape area, away from the windy, often cool, coastal zone, into a less rich floral region, the bee fauna does not become smaller and may in fact become larger.

Floral richness of bee-pollinated plants, such as occurs in the tropics, associated with only moderate bees faunas, is possible because of generalist bees that pollinate many species of plants. In the tropics the outstanding polylectic bees are the highly eusocial *Apis* and Meliponinae, all species of which are active throughout the year and thus not seasonal like flowering of most plants. The Halictinae are another major taxon, abundant in the tropics, most species of which are polylectic.

In an earlier paper (Michener, 1954) I noted geographical variations in the relative abundance of oligolectic species of bees. In the Western Hemisphere the highest percentages of oligolectes are found in the bee fauna of xeric regions like the Sonoran, perhaps lower percentages in prairie areas, certainly lower in mesic eastern North America, and lowest in the moist tropics. Moldenke (1975, 1976a, 1976b) found 60 to 62% of the bee species in California to be oligolectic in different Sonoran desert areas, 50% in the high mountains, 40–50% in Californian areas of Mediterranean climate, and 30% in the coastal strip. Robertson (1929b) found 28% of the species oligolectic in southern Illinois; this figure is high because he studied only a limited area and some of his "oligolectes" are narrowly polylectic when viewed from a broader standpoint. By contrast, a recent year-long study in French Guiana by D. Roubik and the author revealed only one or two percent of the total that were clearly oligolectic in this moist tropical area. Of course, various

uncommon species were collected on only one flower species in the course of a year's collecting. Thus larger numbers of oligoleges could exist but the percentage seemed clearly low.

In 1954 I suggested that in the xeric areas, where flowering tends to be synchronized and where many kinds of bees therefore have overlapping short seasons of flight, so that seasonal segregation is impossible, there are advantages in oligolecty, which divides available food resources (probably limiting in some years) among species and reduces interspecific competition for those resources. In the tropics, at the other extreme of the series, many species of bees have long seasons of flight or are active throughout the year, and the plants' flowering periods are scattered and sometimes long. There is no season without flowers. The abundance of individual bees at any given time is usually much less than at the season of major flight in the Sonoran or Chihuahuan deserts. Most flower species in the tropics are not in bloom for as long as the flight periods of most bees, so that oligolecty is often impractical. Areas like the eastern United States are intermediate, with a long period (e.g., March to September) when bees are active, different species flying at different seasons. With such seasonal segregation, even rather broadly polylectic bees are often prevented from competing, and there is thus less pressure than in the deserts for oligolecty as a device to partition resources.

These ideas seem compatible with Moldenke's (1976b) conclusions that in California, areas with the largest bee faunas have the highest percentage of oligolecty, and those with the fewest species of bees have the lowest percentage of oligolecty (my definition of the term). We seemingly agree that the larger the number of species that is in flight during the same season of the year, the higher the percentage of oligolectic species.

It is not clear whether information from outside of the Americas supports these hypotheses and interpretations. We need data on such matters as the following: Is the percentage of oligolectic bee species higher in the Mediterranean basin than in central Europe? Is the percentage of oligolectic bee species higher in western South Africa than in equatorial Africa? (My subjective answer to the last question, based on a few months' collecting in each area, is *yes*.)

A reasonable criticism of the ideas presented above is that the high frequency of oligolecty in the xeric, warm temperate areas has been documented only for the Western Hemisphere and is due largely to Panurginae. Since most panurgines are oligolectic, and since they are especially numerous in the xeric warm temperate areas of the Western Hemisphere and particularly scarce in the tropics, their mere existence might lead to the described geographical variation in percentage of oligoleges in the bee fauna. If one eliminates the Panurginae, however, there are still high percentages of oligolecty in the western United States compared to the East, and the low percentage in the tropics remains unchanged.

The distribution of an oligolectic bee may on occasion be limited by the distribution of its pollen source. For example, before its dispersal by man, the genus *Cucurbita* was probably not found east of a line through east Texas and central Kansas, except for a species in Florida. Man dispersed *Cucurbita* as a crop plant, and now one species of *Peponapis* and two of *Xenoglossa*, oligolectic bees on this plant, range to the Atlantic coast, the *Peponapis* reaching New England (Hurd &

Linsley, 1964). Apparently the bees had the potential to withstand the climate far beyond the natural range of their host plant, for they have now expanded their ranges by half the width of the continent. There is no evidence that the plant is limited by its oligoleges. Where it is introduced in the absence of its oligoleges, polylectic bees provide pollination.

Similar examples on a smaller scale are not uncommon. Thus *Prochelostoma philadelphi*, an oligolege on *Phildalephus*, occurs in gardens well beyond the range of native plants of this genus, for example, in Lawrence, Kansas. This is some 300 km northwest of the natural range of *Philadelphus*.

Very often, plants extend beyond the ranges of their oligolectic bees and also occur, within the general ranges of the bees, in local populations lacking such bees. For example, the boraginaceous genus *Cryptantha* ranges widely over the western United States, east to Kansas, and south in Mexico and into South America. A few species of the genus *Andrena* and all species of the megachilid subgenus *Proteriades* and its close relatives have short, hairy mouthparts morphologically adapted to extract pollen from the very small flowers of *Cryptantha*, and are usually considered as oligolectic visitors of *Cryptantha* (Timberlake & Michener, 1950). [In spite of what appear to be clear morphological adaptations for collecting pollen of *Cryptantha*, however, some species of *Proteriades* at some times (perhaps when *Cryptantha* is scarce) use pollen from other sources in provisioning their cells (Parker, 1978). It may be that most oligolecty breaks down on occasion.] These *Cryptantha* oligoleges are primarily Californian, although some *Proteriades* range, as rare, localized populations, as far east as the Dakotas and New Mexico. It is obvious that the plant can get along with general (polylectic) pollinators and is not dependent upon oligoleges. As noted by Linsley et al. (1973), bee pollination frequently has played only a minor role in plant evolution despite specialization and oligolecty of some of the bees. Even when there appears to have been coevolution of plant and bee as in some species of *Clarkia* and its oligoleges, there appear to be populations of the plants without the oligolectic visitors but pollinated by polyleges (MacSwain et al., 1973).

Another illustration of the same thing can be deduced from the *Larrea divaricata-tridentata* species pair, an amphitropical bush found in deserts of both North and South America. In both continents it has oligolectic (in North America, monolectic) bee visitors, but they belong to different genera in the two hemispheres. For example, various oligolectic species of *Perdita*, *Nomadopsis*, *Ancylandrena*, *Megandrena*, *Hesperapis*, *Emphoropsis*, *Heteranthidium*, and *Hoplitis* visit flowers of North American *Larrea* (Hurd & Linsley, 1975), but these genera do not occur in South America. Other species of *Larrea* are all South American, and it seems likely that the genus jumped across the tropics in geologically very recent times to become established in Mexico and the southwestern United States. It could not have come with its South American oligoleges. Therefore it must have survived in North America for a long time, being pollinated by the general pollinators (polyleges), before its North American oligoleges evolved.

Sometimes oligolectic bees appear to play no role in pollination of their host plants. An example is *Perdita wootonae*, an oligolectic visitor to flowers of *Mentzelia decapetala*. It flies only in the late afternoon when the *Mentzelia* flowers

open. The tiny bees climb out on the long radiating stamens and collect pollen individually from the anthers, and do not usually even approach the stigma (personal observations). They are thus in effect parasites. The whitish flowers are normally pollinated by sphingid moths. Similar observations have been made for *Perdita texana* on flowers of *Opuntia* (Barrows et al., 1976).

From accounts such as the above, one can conclude that sometimes the distribution of a bee species or genus is dependent upon the presence of a particular flower (as in *Peponapis* and *Xenoglossa* on *Cucurbita*). The general distributional limits of the oligolectic bees, and of course also polylectic bees, ordinarily result from climatic factors, barriers to dispersal, and presumably competition with other bees for food or nest sites, not from lack of specific food plants. Plants commonly range more widely than their oligolectic visitors and thus are not dependent upon the latter for pollination. Even outcrossing plant species that have oligolectes commonly reproduce quite well without the oligolectic visitors, thanks to polylectic pollinators.

#### DISTRIBUTIONS OF THE GROUPS OF BEES

In this section the distributional patterns of each group of bees are discussed, and explanatory comments are included where they seem useful. In view of Raven & Axelrod's (1974) treatment of continental movements and associated climatic changes in relation to angiosperm biogeography, I have not repeated information on such movements but have used their summary in attempting to explain, in this and the next section, certain historical aspects of apoid biogeography.

In the following account and in Table 3, I have used certain terms that require explanation for geographical areas. Because bees are so well developed in some of the world's arid areas, these have been segregated and are repeatedly referred to. The abbreviations used for the columns of Table 3 are listed below:

1. Australia (Ast). In Table 3 the following area (2) is segregated. Tasmania is part of the same faunal area but is mentioned separately in the text.
2. Northern Australia and New Guinea (NAt/NG). The northern extremity of Australia, especially where forested, and New Guinea, Bismarck Archipelago, and nearby islands.
3. New Zealand (NZ).
4. Oriental region (Ort). Tropical Asia from Sri Lanka (Ceylon) and the lowlands of India to Viet Nam and southeasternmost China, also Indonesia (except New Guinea) and the Philippines, although these are mentioned separately in the discussion.
5. Madagascar (Mdg).
6. Africa (Afr). Subsaharan Africa except as indicated below (7). Note that Africa as used in the text does not include the north coast of the continent. In Table 3 it also does not include the Cape region.
7. Cape region of Africa (Cpe). The area of Mediterranean climate with Cape macchia plus the more desertic Karoo and the Namib Desert area.

TABLE 3. Summary of distributions of tribes, subfamilies and families of bees. Areas (column headings) are listed in the text. The number of + signs in any row indicate the relative abundance and diversity of that taxon in different areas; comparison of the number of plus signs for various taxa up and down a column is of no value. m = entering an area only marginally, or one species extending well into an area but not half way across it.

	Ast	NAt/ NG	NZ	Ort	Mdg	Afr	Cpe	Pal/ arc	Med/ CA	Ne/ arc	Mad	Neo/ tro	Ant	Arg/ Brz	Ara
Euryglossinae	++														
Hylaeinae	+++	++	+	+	+	+	+	++	+	+	+	+		+	
Xeromelissinae										m		+		+	++
Paracolletini	+++	+	+				+				+	+		++	++
Colletini							+	+	+	+	+	+	+	+	+
Diphaglossinae										m	+	+	+	+	+
Stenotritinae	+										+	+			
Oxaeidae										m	+	+		+	
Dufoureae				+		+	+	+	+	++	+				+
Nomioidini	+	+		+	+	+	+	+	+						
Augochlorini											+	+	+++	+	++
Halictini	++	+	+	+	+	++	++	+++	+++	+++	++	+	+	+	+
Nomiinae	++	+		++	++	+++	+	+	+	+	+		+		
Andreninae						+	+	+++	++	+++	++	m			+
Panurginae					+	+	+	+	+	+++	+++	+		++	++
Macropodinae								+	+	+					
Ctenoplectrinae		+		+		++		m							
Melittinae						+	++	+	+	+	+				
Dasypodinae							++	+	+	m	+				
Fideliidae							+								+
Lithurginae	+	+		+	+	+	+	+	+	+	+	+	+	++	++
Megachilini	++	+		+	+	++	+	++	++	++	++	++	+	++	+
Anthidiini		m		+	+	++	++	+	++	+	+	+	+	+	+
Dioxini							+	+	++	+	+				
Xylocopini	+	+		++	+	++	+	+	+	+	+	++	+	+	m
Ceratinini	m	+		++	+	+++	+	+	+	+	+	++	+	+	+
Exomalopsini- Ancylini				m					+	+	+	++	+	+++	+
Pararhophitini									+						
Tetrapediini												+			

TABLE 3. *Continued.*

	Ast	NAt/ NG	NZ	Ort	Mdg	Afr	Cpe	Pal/ arc	Med/ CA	Ne/ arc	Mad	Neo/ tro	Ant	Arg/ Brz	Ara
Melitomini										+	+	+		+	+
Eucerinodini															+
Canephorulini														+	
Eucerini				+	+	+	+	+	+	++	++	++	+	+++	++
Anthophorini	+	+		++	+	++	+	++	+++	++	++	+	+	+	+
Melectini	+	+		+		+	+	+	++	+	+		+		
Centridini										m	+	++	+	+	+
Ctenioschelini										m	+	++	+	+	+
Rathymini												+			
Nomadini	m	+		+		+	+	++	+	++	++	++	+	++	+
Epeoloidini								+		+					
Protepeolini											+	+		+	
Isepeolini														+	+
Caenoprosopidini														+	
Neolarrini										+	+				
Townsendiellini											+				
Ammobatini					+	+	++	+	++	+	+				
Holcopositini								+	+	+	+				
Biastini								+	+		+				
Ammobatoidini								+	+						
Meliponinae	+	+		++	+	++						+++		++	
Euglossini												++	+	+	
Bombini				+				+++	+	++	+	+		+	+
Apinae				++	+	+	+	+	+						
Total taxa	15	15	3	18	15	23	23	29	29	33	34	28	17	27	24

8. Palearctic region (Pal/arc). The palearctic faunal region. In Table 3 the following area (9) is excluded from the Palearctic.

9. Mediterranean Basin through Asia Minor to desertic areas of Central Asia (Med/CA). Includes the Canary Islands, Azores, etc.

10. Nearctic region (Ne/arc). The Nearctic faunal region. In Table 3 the following area (11) is excluded from the Nearctic.

11. Madrean region (Mad). The areas of California having a Mediterranean climate, mostly with macchia or chaparral (Californian), plus the more desertic areas from southern California to west Texas and south through the Mexican plateau. This includes the Chihuahuan and Sonoran deserts. The term Madrean is derived from the works of Axelrod (e.g., 1958).

12. Neotropical region (Neo/tro). The Neotropical faunal region, from tropical Mexico southward. In Table 3 the regions listed below (13–16) are all excluded from the Neotropical.

13. Antilles (Ant). The Greater Antilles, except when the Lesser Antilles are specifically mentioned.

14. Temperate South America. The next two regions (15, 16) together.

15. Argentina-southern Brazilian area (Arg/Brz). The area of temperate Brazil and adjacent countries, south into Argentina, including the central desertic parts of Argentina.

16. Araucanian region (Ara). Chile and the adjacent parts of southern Argentina (Ringuelet, 1961).

The data in the following more detailed verbal account are summarized at the tribal to family levels in Table 3.

#### COLLETIDAE

This family is considered the most primitive among bees, partly because of the short mouthparts which resemble those of wasps. The family is probably paraphyletic, held together by resemblances which are primitive features. It is difficult to find any derived character common to colletids and not also found in other groups of bees. A candidate for such a character, however, is the secretion by adult females of a cellophanelike membrane to line the cells. Other bees either do not line the cells, or line them with more waxlike materials.

Following Jander (1976) and Michener, Winston & Jander (1978), I assume that the colletid subfamilies Euryglossinae and Hylaeinae which carry pollen to the nest internally, in the crop, are ancestral in this respect to bees that carry pollen externally in a scopa. The pollen-gathering movements of the hylaeines and, presumably, the euryglossines are such that only pollen sticking to the forelegs and head can be swallowed for transport in the crop, while pollen that lodges on the other legs, the thorax, and the abdomen must be largely lost. This seems inefficient. It is unlikely that hairy bees that carry pollen in a scopa, and that can transfer to the scopa pollen sticking to both head and thorax, as well as all the legs, would evolve into forms inefficient in these respects like hylaeines.

Of these two subfamilies, the Euryglossinae are more primitive in various features than the Hylaeinae. The former are found only in Australia, being represented by 27 genera and subgenera, four of which reach Tasmania (Michener,

1965a and subsequent papers by E. Exley). None occurs in New Guinea and the subfamily is scarce in tropical northern Australia. Most species are restricted to or collect pollen primarily from flowers of Myrtaceae (Michener, 1965a). It is therefore possible that the relative scarcity of Myrtaceae in other continents is responsible for absence of Euryglossinae in those continents. There are, however, many Myrtaceae in South America. This plant family appears in the Upper Cretaceous fossil record and presumably migrated across Antarctica, but the euryglossines may not have tolerated such a cool temperate, probably forested route. The climatic tolerance of Euryglossinae appears to be limited, as suggested by the scarcity of the group in cool, moist Tasmania as well as in the tropical north of Australia.

The subfamily Hylaeinae is widespread but is diverse and a major faunal element only in Australia (Michener, 1965a; Houston, 1975), where there are 28 genera and subgenera, *Hylaeus* with 14 subgenera being the largest genus. Of these subgenera three reach Tasmania, one reaches New Zealand, and one has a species in the Tuamotu Islands. Obviously, Hylaeinae are capable of occasional long distance, over-water dispersal. New Zealand species of *Hylaeus* are similar to certain Australian ones and must have arrived relatively recently over water. The distance is 1,600 km, with no significant intervening islands. Although many Australian Hylaeinae occur in temperate areas, the group is most diverse in subtropical and tropical Australia, where most of the forms that are segregated from *Hylaeus* as distinct genera occur. The genus *Palaeorhiza*, while found in subtropical and tropical Australia, is most abundant and diversified in New Guinea, from which it ranges as far west as Timor and Flores and as far east as the Solomon Islands and the New Hebrides. *Gephyrohylaeus* is a small group which ranges from northern Australia to Borneo. No other genus of bees has a similar range.

In Africa there are two distinct hylaeine genera (both unnamed), one in the high equatorial mountains, the other in the Cape region (R. Snelling, in litt.). They have no obvious relations to particular Australian genera, but might be part of the same complex.

The genus *Hylaeus* is worldwide, less diverse in other continents than in Australia, but with a specialized derivative called *Nothylaeus* in Africa and Madagascar. Cladistic relationships among hylaeine genera have not been investigated, but my belief is that *Hylaeus* (or certain groups thereof) is primitive and that most or all of the other genera are derived from it.

There are about 11 palearctic subgenera of *Hylaeus* (Popov, 1939). Thus there is a secondary center of diversity within the genus in that region. One Palearctic subgenus, *Nesoprosopis*, is represented by only one species in Europe but about half of the Japanese species belong to it (Hirashima, 1977); it is found also in the Bonin Islands and in Hawaii. In the latter, extensive speciation (about 60 species) has occurred (Perkins & Forel, 1899).

Three of the Palearctic subgenera are also abundant in the Nearctic region, where two small strictly Nearctic subgenera also occur (Snelling, 1966). Of about five Neotropical subgenera, two reach the southern Nearctic region. The genus is present in the Antilles (Alayo Dolmau, 1973). The African subgenera have not been elucidated in print but there are six of them (Snelling, in litt.), at



least two of which reach Madagascar. Relationships among the subgenera of *Hylaeus* have not been investigated on a world basis, but there is no obvious similarity among the subgenera found in Australia, South America, or Africa. The species of the Oriental region have mostly not been assigned to subgenera (except for *Hoploprosopis* in the Philippines), but they are not numerous and show no suggestion of relationships to Australian forms. Presumably they are of Asiatic origin. The Neotropical and described African forms (including the genus *Nothylaeus*) also seem to be related to northern subgenera (Snelling, in litt.). *Hylaeus* in South America is best represented in tropical and subtropical regions and is absent in the Araucanian region, facts which also argue against an interchange with Australia either directly or through Antarctica.

Australian forms of *Hylaeus* include some with at least certain characters (e.g., pygidial plate) more primitive than in any other Hylaeinae (Michener, 1965a). In view of this and the presence of Euryglossinae in Australia, it is reasonable to suppose that Hylaeinae arose on the southern continents, presumably in Australia. It is not clear how they reached other continents, except that it was not via New Guinea and the Indonesian area to Asia during the last 15 m.y. that the route has been more or less open, for this is too recent and also would require them to traverse a large land area, the Oriental region, where the subfamily is not well represented. The secondary center of diversity in the genus *Hylaeus* in the Palearctic region may have been populated from Africa, or via India across a reduced Indian Ocean, or both, in the early Tertiary and may well have served as the source for the New World, as well as perhaps the present African and the southeast Asian forms of this genus. The best route between southern and northern continents was via northern Africa to Eurasia.

The subfamily and perhaps even the genus *Hylaeus* might have appeared in the Upper Cretaceous (say 70 m.y. BP) and been dispersed by continental movement. Lack of similarity between the Australian and South American faunas, however, argues against this hypothesis, for those continents were connected through cool temperate Antarctica until about 38 m.y. BP. *Hylaeus* lives in such climates at the present time—for example 15 species of various subgenera are known from Finland (Elfving, 1968).

The subfamily most closely related to the Euryglossinae and Hylaeinae is the Xeromelissinae (= Chilicolinae), best developed in the Araucanian region but extending more sparsely into Brazil and north to St. Vincent in the Lesser Antilles and to the southern part of the Mexican Plateau. It seems to be absent from wet lowland tropics but can be found in either dry lowlands such as northeastern Brazil or at middle altitudes such as in the Colombian Andes or the central plateau of Costa Rica. Presumably the ancestors of Xeromelissinae became isolated from those of Euryglossinae and Hylaeinae at least 38 m.y. BP when opportunities for more or less direct migration between Australia and South America via temperate Antarctica no longer existed.

The subfamily Colletinae is divided into two tribes, the ancestral Paracolletini and the widespread Colletini. The Paracolletini, presumably the most primitive (Michener, 1944) of the hairy bees that carry pollen externally on the scopal hairs (in this case on the hind legs and sometimes also on the abdominal sternum),

have a disjunct, largely panaustral distribution. There are 27 genera and subgenera in Australia (Michener, 1965a), two of which reach Tasmania. One Australian subgenus also reaches New Zealand, where it occurs with a closely related subgenus restricted to New Zealand. A different Australian subgenus has one species in New Caledonia. None of the forms occurring in New Zealand or New Caledonia appears to be relictual; rather they must be relatively recent over-water migrants from Australia, to judge by their similarity to Australian forms. To the north one subgenus reaches New Guinea and Misool. The great abundance of species and higher groups, however, is in the temperate parts of Australia, with but few species, all in the genus *Leioproctus*, in outlying regions. The presence of a few species of the genus in New Zealand and one in New Caledonia indicates an ability to cross rather large water gaps. Since *Leioproctus* nests in the ground, such migration must be by bees being blown or possibly clinging to detritus. The only paracolletine known to nest in wood, *Callomelitta*, is restricted to temperate Australia.

The closest relatives of Australian Paracolletini are members of the tribe found in South America. About 17 genera and subgenera are found there. (More have been described; I have estimated that there are 17 more or less equivalent in distinctness to those in Australia.) As in Australia, the genus *Leioproctus* is the predominant group (Michener, 1965a), but none of the subgenera is the same in the two continents. The species are common in the Araucanian Region but also abundant and morphologically diverse in the southern part of eastern South America (southern Brazil to Argentina). In smaller numbers they range north to the arid parts of northeastern Brazil, as well as through the Andes. A single genus, *Eulonchopria*, occurs not only from central Brazil to Argentina but also in arid parts of Mexico and southern Arizona (Sonoran region). This is the only penetration of the Northern Hemisphere by Paracolletini, and the genus is the only amphitropical paracolletine (Michener, 1963). Presumably the separation of South American and Australian Paracolletini dates to at least 38 m.y. BP when more or less direct migration through Antarctica between these two continents became impossible.

The only remaining Paracolletini, the two closely related genera of southern Africa, have some characters in common with the Euryglossinae that indicate either a common ancestor or convergence. The African genera (*Scapter*, *Parapolyglossa*) may have been isolated from those of Australia and South America since Africa, Antarctica, and Australia drifted apart. An interrupted pathway for migration through Madagascar and India from Africa to Australia existed in the Upper Cretaceous, but relatively long distance over-water transport may have been involved in the dispersal of Paracolletini to Africa. Only one successful introduction is necessary to explain all the African Paracolletini. They occur both in the arid Cape region and in mesic eastern South Africa, but are morphologically a compact group. (A parallel is the Restionaceae, likewise homogeneous in Africa; Raven & Axelrod, 1974.)

The tribe Colletini, the sister group of or perhaps a derivative of the Paracolletini, is found on all continents except Australia (also absent from Madagas-

car). There is only one major genus, *Colletes*; it has numerous species in all continents except Australia. *Colletes* probably originated in the south, however. Its only close relative is an unnamed genus of the Araucanian region which contains several species obviously affiliated with *Colletes*, but lacking some of its special features and therefore more like Paracolletini. If *Colletes* arose in South America, as seems likely considering both its Araucanian relative and the distribution of the Paracolletini, it must have spread to other continents via North America or possibly across the narrow Atlantic to Africa and Europe. While land connections between the Americas date only to 5.7 m.y. BP, island hopping would have been increasingly possible from the Oligocene onward, and is very probable considering the abundance and diversity of *Colletes* species in the Holarctic region and the presence of *Colletes* today in the Greater Antilles. Failure of the genus to reach Australia recently by island hopping can be attributed to its absence from southeast Asian lowlands, Indonesia, and even the lowlands of India. It occurs in the lowland moist tropics in the Americas, but not in Asia and probably not in Africa.

The subfamily Diphaglossinae consists of large, robust, fast-flying colletids restricted to the Western Hemisphere (Michener, 1966). The three genera of the tribe Diphaglossini are restricted to the Araucanian region. The two genera of Mydrosomini are tropical forest bees from Brazil to southern Mexico. The monotypic tribe Ptiloglossidiini is from northern Argentina. The tribe Caupolicanini contains seven genera and subgenera. Of these, *Ptiloglossa* is largely tropical, ranging through the moist tropics although extending beyond the tropics both in Argentina and in North America (to Southern Arizona). *Crawfordapis* is restricted to Mesoamerican mountains. The genus with the most interesting distributional pattern is *Caupolicana*. The subgenus *Caupolicana* s. str. occurs in the Araucanian and adjacent parts of South America, with a few species extending well north in Peru, and reappears in the North American deserts, extending to Arizona and beyond, into the plains, to western Kansas. There is also a single species in the southeastern United States. The subgenus *Zikanapis* also has a disjunct amphitropical distribution—southern Brazil and adjacent warm south temperate regions, north in the Andes to Colombia, and the Mexican plateau, north to southern Arizona. The subgenus *Alayoapis* is known only from Cuba and Hispaniola. Seemingly the Diphaglossinae arose in South America, probably from a paracolletine stock, and invaded the Antilles and southern North America during the Tertiary, perhaps by crossing water or in some cases wet tropical areas, as did certain plant families like the Loasaceae and Zygophyllaceae (Raven & Axelrod, 1974: 628).

The only remaining colletid group, perhaps not properly placed in this family, is the subfamily Stenotritinae, consisting of two genera restricted to the temperate parts of Australia (Michener, 1965a).

In summary for the Colletidae, the family is clearly primarily southern, i.e., of Gondwanaland origin, only the genera *Colletes* and *Hylaeus* becoming widespread (the former absent in the Orient and Australia) and now occupying the Laurasian as well as the Gondwanaland continents.

## OXAEIDAE

This is a small family limited to the Western Hemisphere. It contains four genera and subgenera (Hurd & Linsley, 1976) of which *Oxaea* is tropical (Brazil to southern Mexico), *Notoxaea* is southern (South Brazil to northern Argentina), and *Protoxaea* and *Mesoxaea* occur in the North American deserts and on into eastern Texas and Louisiana. The last three taxa are commonly united in a single genus *Protoxaea*, which in this sense is amphitropical. In view of its limited distribution in the Nearctic region, the family is presumably of Neotropical origin.

## HALICTIDAE

This family contains three subfamilies, of which one, the Dufoureae (Michener, 1965b), consists mostly of morphologically specialized forms restricted to particular flowers and often uncommon, but retains a number of ancestral features such as cocoon-spinning by larvae. It is presumably the sister group to all the other Halictidae. It is principally Holarctic, with about eight Palearctic and six Nearctic genera and subgenera, two of them (*Dufourea* and *Halictoides*) in common. The area with the largest number of species and with great morphological diversity is the western United States. From California 74 species are recorded (Moldenke & Neff, 1974); comparable Palearctic areas have only 4 to 8. Of two Palearctic genera, *Systropha* and *Rhophites*, each has a species or two reaching southern Africa, where there is a distinctive subgenus of *Systropha*. *Systropha* also occurs in tropical areas, e.g., West Africa, India, Sri Lanka, and southeast Asia, although it is most abundant in xeric areas of the Mediterranean basin and thence eastward toward central Asia.

In the Western Hemisphere, the northern genera occur south only into the Mexican plateau. There is, however, a geographically isolated genus, *Penapis*, containing two species in Chile. It is possibly most closely related to genera such as *Sphecodosoma* of Texas and the southwestern United States, but is very different, and the two have presumably been diverging for a long time. As no American members of the subfamily are known from the tropics, *Penapis* presumably reached Chile across a substantial uninhabited gap.

The enormous subfamily Halictinae is divided into three tribes. The tribe Augochlorini, containing 31 genera and subgenera (Eickwort, 1969), is primarily Neotropical, with three otherwise Neotropical genera, *Augochlora*, *Augochlorella*, and *Augochloropsis*, extending north in eastern America as far as southern Canada, and two others, *Pseudaugochloropsis* and *Temnosoma*, barely reaching the southwestern United States. Eight genera range from North America to Argentina, and ten are restricted to the area of southern Brazil to Argentina, which thus seems to be the region of maximum diversity for the tribe. This tribe is poorly represented in the North American deserts and only a single species is found in the Pacific coast states. In the Araucanian area, however, it is represented by the genus *Corynura* with two subgenera and rather numerous species. This genus has some characters (e.g., a galeal comb) unusual in halictines and presumably primitive, but it is unrelated to Australian halictines which are all in different tribes. It is likely that aridity and physiographic barriers have made the Arau-

canian area a refuge for this primitive type, which has perhaps disappeared elsewhere in South America, except for the minute species of the related genus *Halictillus* in southern Brazil and Argentina. Augochlorini are well represented in tropical forested areas and four genera have reached the Antilles.

The tribe Nomioidini, containing a single genus *Nomioides*, is found in the steppe, savanna and desertic areas of the Old World from the Canary Islands, the Mediterranean area, and even central Europe, throughout Africa, eastward to Madagascar and across Asia to Taiwan, the Philippines, the Sunda Islands and with a single species reaching middle latitudes in Australia (Michener, 1978a). It is absent from forested areas, including (so far as known) New Guinea and nearby islands. It has obviously crossed rather broad water or forest areas to reach parts of its range.

The tribe Halictini (Michener, 1978a) is represented by many species on all continents. There are seven strictly American genera. One group consists of *Habralictus* and *Caenohalictus* which range from northern Argentina to tropical parts of Mexico (Michener, 1979), the latter genus also occurring in the Araucanian region. The second group consists of the south temperate *Pseudagapostemon*, the Araucanian *Ruizantheda*, the tropical forest genus *Rhinetula*, the Mesoamerican montane *Paragapostemon*, and the widespread (Canada to Argentina) *Agapostemon*. The last is well represented in the Antilles (Roberts, 1972), but absent from the Araucanian region.

Africa has a distinctive group of Halictini (Michener, 1978a), none of which is closely related to those of South America or Australia. *Zonalictus* ranges throughout sub-Saharan Africa and into the Arabian peninsula; *Patellapis* (3 subgenera) is restricted to southern Africa, both arid and savanna regions. *Pachyhalictus* contains only one African species, from Malawi to Natal, but there are numerous Oriental species (India to the Philippines and New Guinea) and even one in northern Australia. *Thrinchostoma*, with three subgenera, occurs throughout Africa except the Cape region, is particularly well represented in Madagascar (where a derived parasitic genus *Parathrinchostoma* occurs), and ranges in Asia from southern India to Viet Nam, Kalimantan, and Java. A final member of the African group of genera is *Thrincohalictus*, not found in Africa but represented by a single species in Asia Minor.

The remaining members of the tribe Halictini are mostly in large, widely ranging genera, 20 or more genera and subgenera being involved. *Lasioglossum* and its subgenera occur on all continents, although relatively poorly represented in the Neotropics where their place is partly taken by the Augochlorini. The six Australian subgenera are all restricted to that region, except that one of them, *Ctenonomia*, ranges to southeast Asia. Another, *Parasphecodes*, extends to New Guinea and a third, *Austrevylaeus*, to New Zealand (Michener, 1965a). Clearly the New Zealand forms are relatively recent over-water arrivals from Australia. Africa also contains a rich fauna with several distinctive groups of *Lasioglossum* (e.g., *Oxyhalictus*), none of them closely related to congeners in Australia or South America. The Holarctic region contains several widespread subgenera with many species—*Lasioglossum* s. str., *Evylaeus*, *Dialictus*, as well as a few more restricted subgenera such as *Sphecodogastra*, which is oligolectic on flowers

of Onagraceae in the western United States, and the parasitic (on *Dialictus*) genus or subgenus *Paralictus* primarily in the central and eastern United States. Neotropical forms, which range all the way to Argentina and Chile, are mostly *Dialictus* with some *Evylaeus*, both groups consisting of species rather close to members of the same subgenera in the Nearctic region and not similar to Australian or African subgenera of *Lasioglossum*. Thus the South American forms must have arrived from the north at some relatively recent time. This could well have been before continental connections developed 5.7 m.y. ago, for these bees are evidently good island hoppers. *Dialictus* occurs on the Antilles, and on such small and isolated oceanic islands as Bermuda and Fernando de Noronha.

*Halictus* with its three subgenera is primarily Palearctic with many species and much diversity in Eurasia. One subgenus, *Seladonia*, extends south throughout Africa, India, and Southeast Asia and also contains a few Nearctic and Mesoamerican species and one that occurs in central Brazil. Another large Palearctic subgenus, *Halictus* proper, contains four Nearctic species representing two Palearctic groups and thus at least two migrations from Eurasia to North America. One of the North American species reaches Colombia and Trinidad and occurs also in Cuba. The third subgenus, the palearctic *Vestitohalictus*, is largely restricted to the Mediterranean and Asiatic xeric regions.

*Homalictus* is a large Australian genus, also particularly richly developed and diverse in New Guinea, with a smaller number of species ranging northwest as far as the Philippines and India. The genus has crossed the water gaps rather readily, for some species are similar throughout this wide area, and some species exist on oceanic islands eastward as far as Micronesia and Samoa. Most of the insular species occur on several islands or island groups (Krombein, 1950). The distinctive genus *Echthralictus* has arisen as a parasite of the local *Homalictus* in Samoa.

Finally, there is the genus *Sphecodes* and its relatives (Michener, 1978b), found on all continents but barely penetrating (2 species) northern Australia from Indonesia or New Guinea. Other continents contain many species. Probably the most primitive species, and those most closely related to similar genera (the Neotropical *Microsphecodes* and *Ptilocleptis*), are South American. There are Chilean species and they are not at all similar to Australian ones but are related to those in other parts of South America. The subgenera of the Holarctic region have not been worked out, but there are obvious similarities between the faunas of the northern continents and also Africa. In Africa there is also a related genus, *Eupetersia*, a specialized derivative of *Sphecodes*, found also on Madagascar, with a species on the Seychelles and another in southern India (Michener, 1978b).

The third subfamily of Halictidae, probably the sister group to the subfamily Halictinae, is the Nomiinae. Its classification has not been well studied. It is primarily a tropical and subtropical group of the Old World, and most of the species are tentatively placed in *Nomia*. The greatest diversity is found in Africa (including Madagascar), but there are a few species in the Mediterranean basin and southern Europe, north to Hungary and southern Germany. Eastward, the group is well represented across southern Asia to China, Japan, the Philippines, New Guinea, the Solomon Islands, and Australia. In Asia most of the groups appear to

be the same as those found in Africa, although *Hoplonomia* is primarily Asiatic but reaching through Indonesia to New Guinea and Australia and westward only to Madagascar, not to Africa. In New Guinea there are three groups not found elsewhere (*Reepenia*, *Ptilonomia*, and *Mellitidia*) or reaching only nearby islands and northern Australia (Michener, 1965a). The principal Australian group, *Austronomia*, also ranges across Indonesia to the Philippines, Taiwan and southern Asia. Its ability to colonize islands is shown by the presence of a species, similar to some of those of Australia, on New Caledonia.

Two nomiine groups (*Epinomia-Dieunomia* and *Curvinomia-Acunomia*) have reached North America, no doubt across the north Pacific at a time of more mild climate than the present. They have diversified to a limited extent, each having several western species and one species reaching or limited to the southeastern states; each has been divided into two subgenera as indicated in parentheses above. Each ranges south well into Mexico, and *Acunomia* has one species in Cuba and the Bahamas (Ribble, 1965). The Nomiinae are otherwise absent in the Neotropical region.

In view of the largely northern distribution of the subfamily Dufoureae and the rich representation of the other subfamilies in the Holarctic region, it seems likely that the origin or at least the initial radiation of the Halictidae was in the Laurasian continents. There were early major invasions of the southern continents, however, followed by extensive radiations, especially of Nomiinae in Africa, of Augochlorini in South America, and of Halictini in all three southern continents.

#### ANDRENIDAE

There are two subfamilies of Andrenidae with very different distributional patterns. The subfamily Andreninae includes the huge genus *Andrena* with probably over 1,000 species distributed throughout the Holarctic area. In North America there are some 35 subgenera. Several subgenera and even a few species are holarctic, indicating multiple dispersals between the two northern continents. There are a number of species in the highlands of east Africa; and a few extend southward, one to the Cape of Good Hope. Even west Africa is not without *Andrena*—there is one on the island of São Tomé in the Gulf of Guinea. In India the genus reaches the lowlands, for example in Punjab, and in southeast Asia it is present in mountains. It is not known from Indonesia, the Philippines, etc. In America, while well represented in the Mediterranean climatic area of California, the genus is scarce in the Sonoran area but extends south in small numbers through Central America, the southernmost record being in savanna areas near sea level not far from the Panama Canal Zone.

Aside from *Andrena*, the subfamily includes *Ancylandrena* and perhaps *Megandrena* (with two subgenera) from the Sonoran desert and semidesert (Zavorzink, 1974) and the highly disjunct small genera *Orphana* and *Euherbstia* from Chile (Rozen, 1971).

The Panurginae is a diversified group with many genera. The subfamily is most abundant and diverse in the Western Hemisphere, there being about 38

genera and subgenera in the Nearctic region (including the genus *Perdita* with some 500 species in 20 subgenera) and over 20 genera and subgenera (some undescribed) in the Neotropics. The subfamily is present but poorly represented in the lowland and even montane tropics (Michener, 1954; Friese, 1916, 1921), but there is evidence of north-to-south or south-to-north dispersal of various groups at different times. The panurgines with most ancestral characters occur in both North and South America. Examples are *Psaenythia* in South America and its relative *Protandrena* in North America, and *Cephalurgus* and *Pterosarus* (not similar to one another) in South and North America respectively. Drs. J. G. Rozen and H. Toro (in litt.) suggest that from such basic groups *Heterosarus* arose; it or close relatives range from Canada to Argentina, although they are scarce in the tropics. A derived group of related genera found in both continents contains *Nomadopsis*, *Hypomacrotera* and *Calliopsis* in North America and *Acamptopoeum* and probably *Liopeum* in South America. *Calliopsis* includes a species ranging as far south as Panama and *Acamptopoeum* includes a species that ranges as far north as Colombia.

Since some of the relatives in the two continents are quite different from one another, it seems certain that some of the dispersal occurred well before there were continental connections (5.7 m.y. BP). Most panurgines occur in rather xeric or at least not forested situations. In North America, most species and genera are western and especially southwestern. Presumably there was migration by island hopping between the American continents, but if so, conditions were perhaps rather different from those of the present, for panurgines are not known from the Antilles and are not common in Central America (only two Panamanian species, Michener, 1954) or northern South America.

Outside of the Americas the Panurginae is a small group consisting of about nine genera and subgenera in the Palearctic region (one of them, *Panurginus*, found also in the Nearctic) and four genera in eastern and southern Africa. *Meliturga*, one of the genera found in Africa, is also widely distributed in the Palearctic and two others, *Meliturgula* and *Poecilomelitta*, range into the Arabian peninsula (Baker, 1972), the latter also to Iran (Popov, 1967b). *Meliturgula* also occurs in Madagascar.

The family Andrenidae is absent in Australia, the Indonesian region, and most of southeast Asia.

Probably the family Andrenidae arose or initially radiated in the Laurasian continents, the main area of occurrence of the Andreninae. When genera rather than species are considered (3 genera in North America, 2 in South America, only one in the Old World), the Western Hemisphere seems to take on special importance for the Andreninae, as for the Panurginae. However, except for *Andrena*, all the genera are small, perhaps relictual, and many show little about their areas of origin. The Panurginae, like the Augochlorini in the Halictidae, probably reached South America early in the Tertiary, and there radiated, various lines eventually returning to and reradiating in the Nearctic region, some genera probably then going back to South America, and a few genera spreading from North America to the Old World.



## MELITTIDAE

This is a small family, although divided into four subfamilies. Of all the families of short-tongued bees (i.e., this and previously discussed families), this is the only one sharing certain characters with the long-tongued families, e.g., the form of the mentum and submentum. It is therefore assumed to be an archaic group, either the sister group to all the long-tongued bees or a paraphyletic group from which the long-tongued bees arose.

The Macropodinae contain a single small Holarctic genus with a Chinese species placed in a separate subgenus. The subfamily Ctenoplectrinae contains a single Paletropical genus which is widespread in Africa, where there is also a parasitic subgenus, but is absent in the southwestern Cape region as well as in Madagascar; it occurs also in southeast Asia, the Philippines, Indonesia, New Guinea, and northern Australia. The genus ranges well north into the temperate parts of China and even into the maritime USSR (Popov, 1956); otherwise it does not occur in the Palearctic region.

The remaining subfamilies, the Melittinae and Dasypodinae, are both more common in Africa, especially southern Africa, than elsewhere in the world. Each is represented there by a small number of genera and subgenera. Each is absent from the moist tropics, although *Meganomia* in the Melittinae occurs in equatorial savannas of east Africa as well as in southern Africa. The Melittinae range also through much of the Holarctic region, being represented by several subgenera of *Melitta*. They are less abundant in North America than in Eurasia. The Dasypodinae are represented in the Palearctic region by one widespread genus, *Dasypoda* (Europe to Japan, especially abundant in semiarid areas like the Mediterranean basin). The most interesting distributional pattern in the family is that of the dasypodine genera (or subgenera) related to *Hesperapis*. *Hesperapis* is in the western United States and northern Mexico, with one or two species ranging into the plains and as far north as North Dakota; *Capicola* and its close relatives, in South Africa (mostly Cape Province); and *Eremaphanta*, in arid parts of central Asia (Popov, 1957) such as Turkestan. Regardless of the rank (generic or subgeneric) of these bees, they constitute a group with a highly disjunct distribution, being found in three widely separated arid areas of the world. The family is absent from Australia (except one *Ctenoplectra* in the far north), South America and Madagascar; except for *Ctenoplectra* the family is also absent from southern Asia and nearby islands.

I believe that the Melittinae and Dasypodinae are clearly related and quite likely of African origin, from which continent they reached Eurasia, and thence North America in small numbers. The Macropodinae, entirely Holarctic, and the Ctenoplectrinae, centered in Africa and extending thence to the Oriental and Australian areas, may or may not be closely related to the first two subfamilies.

## FIDELIIDAE

This small family appears to be the sister group to the Megachilidae. It contains only three small genera, two (*Fidelia* and *Parafidelia*) living in arid western parts of southern Africa, the other (*Neofidelia*) living in arid central Chile. The

last direct migration route between Africa and South America was closed about 90 m.y. BP, in the lower Upper Cretaceous, and in any case, was through the tropics. The family must have had a wider distribution in Upper Cretaceous and Paleogene time, and dispersed across oceans which were, however, narrower than at present. There are very few links between the floras of temperate South America and Africa (R. Raven, in litt.) and no possibility for direct migration between these areas seems to have existed during the entire history of the group. (Nests are in dry soil; there is no possibility of nests being transported across water.)

[Since this paper was written, Rozen (1977a) has reduced the fidelids to subfamilial rank in the Megachilidae. Because their rank is of little importance for the present account, and because their proboscis lacks distinctive megachilid characters and is more like that of anthophorids, I have not altered the manuscript. The relationship of fidelids to the base of the megachilid stem is clear, however.]

#### MEGACHILIDAE

The Megachilidae (together with the Fidelidae) are the bees in which females of nonparasitic species transport pollen on the ventral abdominal brush or scopa and not on the hind legs. The family is divisible into two subfamilies, the Lithurginae and the Megachilinae. The former retains a number of ancestral characters also found in other families of bees, but it also possesses derived features of its own showing that it is a holophyletic sister group of the Megachilinae. The Lithurginae are most diverse in temperate South America where they are represented by the largely Araucanian genera *Lithurgomma* and *Trichothurgus* (Moure, 1949). All continents are inhabited by a few species of the remaining genus, *Lithurge*, which occurs in dry to moist tropical to temperate areas. One subgenus is restricted to the Western Hemisphere, where it is absent in forested tropical regions and is therefore amphitropical. It is present in the Antilles. The other subgenus is found in Europe, Asia, Africa, and Australia and intervening islands, also in New Caledonia and all the island groups eastward to Tahiti (Michener, 1965a) and Micronesia (Krombein, 1950). It also contains a species in northeastern Brazil. Obviously the species of *Lithurge*, which nest in old wood, have been good at crossing water. However, there are few if any insular endemics. Some of the dispersal may have been by primitive man.

The subfamily Megachilinae contains the tribes Megachilini and Anthidiini, both widespread and with numerous genera and subgenera, and the tribe or divergent anthidiine group Dioxini, of more limited range. Few Megachilinae exhibit disjunct or otherwise unusual distributions.

We consider first the relatives of *Megachile*, i.e., those Megachilini without arolia. Of 16 subgenera of *Megachile* in the Nearctic region, three occur also in the Palearctic and eight occur also in the Neotropics. Of these eight, six are primarily Neotropical and have only one Nearctic species or reach only the southernmost United States, and two are primarily Nearctic with a few Neotropical species. In all there are 17 Neotropical subgenera, most of them restricted to that area (Mitchell, 1943). Of seven African subgenera (Pasteels, 1965), one (*Eu-*

*tricharaea*) is wide-ranging in the Palearctic, Oriental, and Australian regions, the others probably restricted to Africa (although the southern Asian and Madagascar species have not been classified subgenerically and may include some members of African subgenera). As to Australian subgenera, in addition to *Eutricharaea*, one is restricted to Australia and another ranges from northern Australia to south-east Asia and India (Michener, 1965a).

The genus *Creightonella* is most common and diverse (2 subgenera) in Africa but also extends across southern Asia from India to southern China and southeast Asia, and on as far as New Guinea and the Solomon Islands.

*Chalicodoma*, consisting of *Megachile*-like bees not equipped to cut leaves, is primarily Paleotropical but there are several Mediterranean species and one that reaches central Europe. There are 13 African subgenera (Pasteels, 1965), two or three of which are also Palearctic, two of which range to southern Asia, and one of which, *Callomegachile*, occurs not only in Africa but all the way from India to Japan, Taiwan, the Philippines, New Caledonia, and the northern half of Australia. There are eight subgenera in Australia (Michener, 1965a), two of which range across Indonesia to southeast Asia, one (*Callomegachile*) far beyond as indicated above. A ninth subgenus in the Australian region ranges from New Guinea to Japan.

The groups listed above, related to *Megachile*, have distributions that suggest dispersal could have occurred during a period when the continents occupied more or less their present positions. Each taxon that occurs on more than one continent or in more than one zoogeographic area occupies neighboring continents or areas. The only exception is noteworthy and not easy to explain. The only American group of *Chalicodoma* is *Chelostomoides*, a widespread Nearctic subgenus especially well developed in the Madrean region, and with a few species in Central America and northern South America. It is absent in southern South America. Strangely, it is almost identical to the large subgenus *Hackeriapis* of Australia (two species in New Guinea savanna areas). There seems to be no evidence for or against any of the likely explanations for this disjunction. Since all the other subgenera of *Chalicodoma* occur in the Eastern Hemisphere, it seems very probable that *Chelostomoides* came in some way from that hemisphere.

*Megachile*-like bees have been excellent island-hoppers. There are numerous species of several groups on the Antilles; numerous species range widely through Indonesia; *Megachile* species (subgenus *Eutricharaea*, which is also African, Palearctic, Oriental, and Australian in distribution) extend to New Caledonia and eastward on all island groups to Tahiti, Micronesia, and Hawaii. There is little island endemism, suggesting recent dispersal, but some of the Pacific species do not appear to occur on any continent. None occurs in New Zealand.

The only remaining genus of Megachilini without arolia is *Coelioxys*, most species of which are parasites in the nests of the megachiline genera listed above. Worldwide studies of its groups are even less complete than for *Megachile*. *Coelioxys* is especially abundant in South America, and 14 subgenera have been named for the species of the Western Hemisphere (Mitchell, 1973). Two such subgenera are Holarctic while four are mostly Neotropical but extend into the

Nearctic region. The remainder are either strictly Nearctic (3) or strictly Neotropical (5). Two of the Neotropical subgenera have species on the Antilles.

In the Old World there is perhaps greater morphological diversity among subgenera than in the New World, but there are fewer recognized subgenera (only 3 in Africa, Pasteels, 1968). One, *Hemicoelioxys*, is monotypic and known only from tropical Africa. Another, the very distinctive *Liothyrapis*, occurs in Africa, the Mediterranean basin, and eastward across southern Asia to the Philippines, New Guinea, and Australia. The third is perhaps a catch-all. Unlike *Megachile* and *Chalicodoma*, *Coelioxys* is poorly represented in Australia and does not extend to Pacific Islands beyond the Solomon Islands and the Philippines.

The remaining Megachilini, those with arolia, have a generally different distributional pattern, being primarily Holarctic and for some groups also African. *Osmia* is Holarctic, four of its subgenera (*Osmia* s. str., *Melanosmia*, *Chalcosmia*, *Diceratosmia*) occurring in both northern continents. Several other subgenera are restricted either to North America or to Eurasia. *Hoplitis* (including *Anthocopa*) is also largely Holarctic, and two of the subgenera, *Alcidamea* and *Formicapis* (the latter perhaps a distinct boreoalpine genus of one species), are Holarctic. *Hoplitis* extends southward to southern India and through east Africa to Cape Province. *Hoplitis* also appears to be ancestral to a variety of taxa in the xeric warm temperate regions such as California, the Sonoran region, the Mediterranean basin, Turkestan, etc. In the southwestern United States there are about 13 such xeric-adapted genera and subgenera, several of them falling under the genera *Ashmeadiella* and *Proteriades*. The Old World xeric segregates of *Hoplitis* superficially resemble some of those of the New World but appear to be independently derived. Some such as *Protosmia* may not be segregates, but may be sister groups to *Hoplitis*; the Pacific Coast (North America) *Chelostomopsis* may be an American *Protosmia* (Popov, 1961). Like *Osmia*, *Hoplitis* does not occur in southeast Asia, Australia, or the Neotropical region.

*Heriades* is a widespread genus. It occurs throughout the Holarctic area and is unusually abundant and diversified in Africa, where a few related genera or subgenera occur. *Heriades* is present in Madagascar. Some of the African species seem closely related to European species. It may be that neither of the two American subgenera occurs in the Old World. In the Western Hemisphere *Heriades* extends southward to the Antilles (Alayo Dolmau, 1973) and Panama. In the Eastern Hemisphere, it ranges widely in the Oriental region and eastward to the Philippines and Micronesia (Krombein, 1950), but while it occurs in Borneo and Java, it is not known from the Lesser Sunda Islands, or other areas to the south and east.

*Chelostoma* is a Holarctic genus with a disjunct distribution in the middle latitudes, in America not or scarcely entering Canada and only marginally entering the Sonoran area. In this continent it is restricted to the west but in the east is replaced by the closely related derivative called *Prochelostoma*.

The tribe Anthidiini has been divided into no less than 80 genera and subgenera in the Old World (Pasteels, 1968) and about 37 in the New World (Michener, 1948). The splitting has been more intense in the Old World, but nonetheless the tribe appears actually more diverse there than in the New World. The

majority of groups (26) are Mediterranean and Near Eastern, often extending to Central Asia, sometimes to east or even southern Africa. Only two groups are tropical west African, but several are found in east Africa and about 20 are largely or wholly restricted to southern Africa. Only a few African groups jump to India and southeast Asia, a distributional pattern common in the Megachilini. There are a few groups in tropical Asia (Pasteels, 1972), only one of which (*Pycnanthidium*) extends across Indonesia to the Solomon Islands and northern Australia. Otherwise Australia lacks Anthidiini. Madagascar has only one anthidiine; its relationships are with African forms.

Only three Palearctic genera reach the New World. One is *Anthidium*, a genus of arid to humid areas in the Holarctic and Neotropical regions as well as in India. The others are *Anthidiellum* and *Trachusa*, both of which are temperate climate genera (although the first ranges far into the American tropics); the American forms are sometimes placed in different subgenera than the Old World forms. In the Americas there are more groups in the moist tropics than in the climatically equivalent parts of the Old World. While there is some diversity in the Madrean area, and some genera are largely restricted to this region (*Heteranthidium*, *Heterostelis*), there is no such diversity as in the climatically equivalent Mediterranean and Asia Minor. The same is true of temperate South America. There are no striking disjunct distributions, except perhaps for *Bothranthidium*, found from southern Brazil to Northern Argentina and in northeastern Mexico. It has recently been taken in savanna areas of Costa Rica, however, so it may not be amphitropical; perhaps it occurs in drier areas across the equatorial region.

The anthidiines most like Megachilini and other bees, and hence probably most similar to ancestral anthidiines, are *Trachusa* and its subgenera (Pasteels, 1972). This group is primarily Palearctic although two subgenera (one, the Holarctic *Trachusa*) occur in the Nearctic region. It therefore seems likely that the tribe is of Palearctic origin. Peters (1972), however, shows that the South African *Aspidosmia* is an anthidiine, and argues that it has important ancestral characters.

There are no anthidiines in the Antilles. This fact, their scarcity on Madagascar in spite of several east African groups, and the extension of only one group eastward beyond Borneo and other continental islands of Asia, suggest that Anthidiini are far less effective in traversing water barriers than are the Megachilini. Nonetheless, the moderately rich South American fauna cannot have developed since the elevation of the present continental connection (except for the South American species of *Anthidium*), and shows no relation to the African (or the almost nonexistent Australian) fauna. Hence the present South American fauna, especially that of temperate South America, must have originated from earlier Tertiary island-hopping immigrants from North America or from transatlantic immigrants from Africa.

The tribe Dioxini consists of seven genera, all parasitic on other megachilids (Popov, 1947). All are Palearctic (mostly Mediterranean and eastward into arid parts of Asia), one of them, *Dioxys*, also occurring in western North America.

In summary for the family Megachilidae, the archaic subfamily Lithurginae may have originated in South America, where it is now most diverse. Its sub-

sequent dispersal was very broad and details cannot even be guessed at. The Anthidiini experienced their main radiation in the Palearctic and African regions; the ancestral forms like *Trachusa* are mostly in the former area, and it is likely that the tribe originated there and spread to other continents. The Dioxini no doubt also originated in the Palearctic, whence they spread to western North America. The osmiine Megachilini are primarily Holarctic and must have originated there, probably, like Anthidiini, in the Palearctic. The other (anaroliate) Megachilini are diverse in all continents and their area of origin or even principal areas of radiation cannot be identified.

#### ANTHOPHORIDAE

This large family consists of three subfamilies, the Anthophorinae, Nomadinae, and Xylocopinae. The Anthophorinae are a major subfamily of long-tongued bees, common and with many genera on all continents except Australia, where they are represented by only two genera. Zoogeographically the most interesting anthophorines are the Exomalopsini with the related or synonymous Ancylini. The former tribe is American, the latter Palearctic; the relationships need to be investigated but the Ancylini appear at present to differ from the Exomalopsini chiefly in distribution.

Of the 26 American genera and subgenera of Exomalopsini (Michener & Moure, 1957), at least 11 are restricted to temperate southern South America, the rest are widespread in the Neotropics or occur farther north in South America. Some genera, especially *Paratetrapedia*, occur abundantly in the wet tropics. Five groups, all subgenera of *Exomalopsis*, reach the southern United States, two of them being primarily desertic or Madrean and not or scarcely occurring in the Neotropics. One of these five also occurs in the Antilles and southern Florida, another reaches the central United States. The Old World representatives of the group, *Ancyla* and *Tarsalia*, occur in the xeric Mediterranean to Central Asian belt, *Tarsalia* curiously with a species in southern India also.

Whereas there are many distinctive exomalopsine genera and subgenera endemic to the southern temperate zone in South America, the climatically equivalent northern region contains only two endemic subgenera. This suggests a longer history in South America than in North America. The occurrence of *Exomalopsis* in the Greater and Lesser Antilles shows the possibility of intercontinental island-hopping. The last direct connection between South America and Africa was in lower Upper Cretaceous (90 m.y. BP). At the beginning of the Paleocene (about 64 m.y. BP) Africa and South America were about 800 km apart, and if there were islands more or less midway, the breadth of the water to be crossed at one jump would have been less than the present distance from Yucatán to Jamaica. Therefore dispersal between Africa and South America could account for the present Old World distribution of the Exomalopsini-Ancylini. On the other hand, North American Exomalopsini, perhaps adapted to rather arid conditions, could have arrived from South America via islands at any time during the Tertiary, and thence reached the Mediterranean area across the still narrow and island-dotted Atlantic.

The related tribe Pararhophitini (Popov, 1949) ranges from the Mediterranean basin to central Asia. It contains only a single genus, *Pararhophites*.

The tribe Tetrapediini, related to the Exomalopsini, is Neotropical—Mexico to Argentina, mostly in wet tropics. It consists of a single genus with two subgenera.

The tribe Melitomini, also related to Exomalopsini, consists of about eight genera and subgenera (Michener, 1954), all American, ranging from Canada to Argentina and Chile. Most of these taxa are either Nearctic or temperate South American, but *Melitoma* ranges through the tropics (South Dakota to Argentina). *Ptilothrix* and *Dasiapis* (a subgenus of *Diadasia*) are amphitropical, occurring in temperate parts of both North and South America, but absent in much of the tropics. The genus *Diadasia* as a whole also approaches such a distribution since it has both North and South American temperate subgenera (in addition to *Dasiapis*); it is, however, represented in the tropics (at least Panama and Brazil) by one small, rare subgenus, *Diadasiana*.

The tribe Eucerinodini contains a single Araucanian species while the Canephorulini contains one species from the desertic parts of Argentina.

The Eucerini is a large tribe well represented on all continents except Australia. The tribe is best represented in the Americas, where 53 genera and subgenera are recognized (Moure & Michener, 1955; LaBerge, 1957). In the Old World there is quite clearly less diversity than in the New World, but no comparative studies at the genus and subgenus levels have been made. It is therefore only possible to give some impressions about Old World forms.

About 25 genera and subgenera are known from the Nearctic region, several of them only entering its southern fringes (LaBerge, 1957). About 33 genera and subgenera occur in the Neotropics, mostly in southern South America but a few restricted to or extending through the tropics. *Alloscirtetica* is the best example of a temperate South American genus; it is richly represented in the Araucanian area but occurs also in other temperate southern areas. Several genera (*Peponapis*, *Svastra*, *Melissodes*, *Florilegus*) are widespread both in North and South America, although *Florilegus* is more abundant and diversified in South America and *Melissodes* far more abundant and diversified in North America. *Martinapis* occurs in the Sonoran and Argentine deserts, not in intervening areas, and there is a tendency toward such an amphitropical distribution in *Gaesischia* which seems to be absent in the wet tropics although present for example, in savanna areas of Costa Rica and in arid northeastern Brazil. In both *Martinapis* and *Gaesischia* the northern and southern representatives are in different subgenera, suggesting long isolation.

The numerous groups that must have dispersed between the American continents and the considerable evolution that has occurred in each continent suggests that part of the interchange must have occurred well before the union of the continents, presumably by way of island stepping-stones. That this is likely is indicated by the presence of five groups, *Ptilomelissa* (a subgenus of *Melissoptila*), *Florilegus*, and three subgenera of *Melissodes*, on the Antilles. All are widespread groups and the species on the islands are similar to those found on the continents.

Two of the North American groups (*Tetralonia-Synhalonia* and *Xenoglossodes-*

*Tetraloniella*) seem to be holarctic, although sometimes different names for them are used in the two northern continents, and the systematic relationships have not been properly clarified. The Palearctic *Eucera* is close to *Tetralonia*. Both *Eucera* and *Tetralonia* occur in the cool northern temperate areas or in early spring in warm temperate, xeric areas, and it is not surprising that this group has passed between the two northern continents. There are two or three other Palearctic genera that show no obvious relationship to American genera.

Eucerini are scarce in the Oriental region although the genera *Melissina* and *Thygatina* are present in Sri Lanka and the Indian peninsula. The tribe is absent in Malaysia and Indonesia. In Africa there is the apparently distinctive genus *Eucera* (with an undescribed species in south India), plus various species currently left in *Tetralonia*, probably only for lack of adequate study. There are similar species in Madagascar. None of the African forms shows close relationships to species of other continents.

The Anthophorini, unlike the Eucerini, are most common and diversified in the Old World (Lieftinck, 1966), but are widespread also in the New World. *Anthophora* is primarily Palearctic, especially abundant in the Mediterranean basin and similar arid warm temperate Palearctic regions, although apparently also widespread in Africa, and rather well represented in North America, including the Madrean region, with a few species reaching the Antilles as well as southern South America. It appears to be rare or absent in much of the intervening American tropics, although present in the Andes. While present in India, it does not occur in Indonesia or farther eastward. *Heliophila* is Palearctic, mostly in arid areas; *Clisodon* is northern Holarctic. In the Old World tropical and south temperate regions (Africa, Southern Asia, Australia, and intervening insular areas eastward to the Solomon Islands) the principal genus is *Amegilla*, which also has a few species in the southern Palearctic. The subgenus or related genus *Asaropoda* is centered in Australia but with a few species extending northward through Indonesia. There is also a series of smaller genera found mostly in warm north temperate, subtropical and northern tropical zones around the world. These are *Deltoptila* in Mesoamerica, *Emphoropsis* in the Nearctic region, *Habropoda* in the Mediterranean region to China, Taiwan, Viet Nam, and India, *Habrophorula* in southeast China, and *Elaphropoda* in the Oriental region, eastward to Java. Finally there is a group (*Pachymelus* and allies) with various Malagasy species but occurring also on the African mainland.

The Melectini consists of bees that are social parasites in the nests of Anthophorini. Not surprisingly, melectine distribution shows similarities to that of Anthophorini. There are eight genera and subgenera in the Old World. *Melecta* is Holarctic, best represented in the Mediterranean area and eastward in arid parts of Asia. *Thyreus* is widespread in Africa, the southern Palearctic region, the Oriental region, and southeast as far as the Solomon Islands and Australia. Of the remaining Old World genera, one is Oriental, two are east and south African, the rest are Palearctic (Lieftinck, 1972).

There are six genera and subgenera in the Nearctic region, all but *Melecta* s. str. being restricted to western North America. Remarkably enough there is an



additional isolated genus, *Nesomelecta*, in the Greater Antilles. Otherwise the tribe is absent in the American tropics.

The tribe Centridini is largely restricted to the American tropics. *Epicharis* (with nine subgenera) is quite strictly tropical while *Centris* with 12 subgenera (Snelling, 1974) is largely tropical. For both genera the area of greatest abundance and perhaps of diversity is the moist tropics. However, *Centris* extends south into temperate South America (both the Araucanian area and Argentina) and north into the Madrean region and marginally beyond, to eastern Texas, Kansas, etc. Several subgenera occur largely or wholly in these xeric areas. *Xerocentris* is amphitropical, being absent in the tropics but present in the North American deserts and in the Araucanian area, while *Paracentris* has a similar but somewhat wider distribution; its presence in the Colombian Andes narrows the gap between its northern and southern areas. One of the major groups of the tropics, the subgenus *Centris*, occurs in the Antilles and southern Florida; it also penetrates the Sonoran region.

The tribe Ctenioschelini contains parasites mostly in the nests of Centridini. It is most abundant and diversified in the American tropics, especially Brazil, where six genera occur. One of them, *Mesoplia*, ranges south into temperate South America including Chile, another reaches southern Arizona in the Sonoran region, while two occur in the Antilles. A seventh genus, *Ericrocis*, is restricted to the North American deserts and adjacent areas.

The tribe Rathymini contains only the genus *Rathymus*, found in the American tropics from Mexico to Brazil.

The subfamily Nomadinae consists entirely of social parasites or cuckoo bees whose larvae feed in the cells of other bees. Although in the past there has been some doubt as to whether the subfamily is monophyletic, J. G. Rozen (in litt.) reports additional (larval) characters that support its status as a monophyletic subfamily. Except for one or two species of *Nomada* in northern Australia, the subfamily is absent in that continent, but it is present in all other continents and most diverse in the Americas.

The forms that are parasitic on the Exomalopsini, the closest nonparasitic relatives of Nomadinae, are presumably the most primitive Nomadinae. They are in the tribe Nomadini (including Epeolini and Osirini, which more or less intergrade with Nomadini in South America). The genus *Nomada* is represented from Argentina to Mexico and Cuba by the subgenus *Hypochrotaenia*, parasitic in nests of *Exomalopsis*. The only related subgenus, but more like the typical northern *Nomada*, is *Micronomada*, restricted to the Nearctic region but especially well represented in the desert areas. At least some of its species are also parasites of *Exomalopsis* and perhaps halictids while others probably parasitize *Andrena*. Once this latter habit arose in the Nearctic region, *Nomada* had open to it an enormous trophic and geographic opportunity. The Holarctic distribution of various groups of *Nomada* indicates that the intercontinental dispersal occurred under more mild climates than the present, probably when the Bering Strait area was temperate or perhaps across the North Atlantic in the Paleogene. The inter-American dispersal must have been by island hopping well before the continental union, a probability in view of the presence of *Hypochrotaenia* in the Antilles. In

the Old World, *Nomada*, while common in the Palearctic area as in the Nearctic, has spread with small numbers of species through Africa to the Cape, and through the Oriental region and Indonesia to New Guinea and the Solomon Islands and to northern Australia. There are only a few related species from Indonesia eastward; this distribution must be the result of relatively recent dispersal (and probably on halictid hosts as the area is devoid of *Andrena*). No additional genera related to *Nomada* occur in the Old World but in the New World there are *Osiris*, *Odyneropsis*, *Polybiapis*, and others in the moist tropics (Argentina to Mexico), as well as five additional Nearctic genera (three of them in the deserts, primarily Sonoran) and one Araucanian genus (*Kelita*).

The genera related to *Epeolus* are sometimes placed in a separate tribe, the Epeolini. *Trophocleptria* of the moist tropics (Argentina to Costa Rica) is the most like the nomadine group of genera and through *Pyrrhomelecta* (southern United States to northern South America) grades into *Epeolus*, another holarctic holarctic genus like *Nomada* but a parasite of *Colletes*. *Epeolus* also ranges to southern Africa. *Triepeolus* is another large genus, largely Nearctic and parasitic on a variety of bees, especially Eucerini, but with various species extending through the tropics to southern South America. The few Palearctic species placed in *Triepeolus* are little known but probably are *Epeolus*.

Seven or eight other genera of Nomadini, some like *Thalestria* and *Doeringiella* obviously related to *Triepeolus* and *Epeolus*, others less closely related, are found in South America, largely restricted to the southern Brazilian to Argentinian part of the continent.

Other tribes of the subfamily Nomadinae are mostly smaller and more restricted in distribution. Thus the Epeoloidini (one genus, *Epeoloides*) is Holarctic. The Protepeolini range from temperate South America to the North American deserts. The genus *Protepeolus* has two species, one in the North American deserts (south to Guatemala), the other in the arid parts of central Argentina (Eickwort & Linsley, 1978). Another genus (*Leiopodus*, only tentatively included in the tribe) is tropical American. The Isepeolini (one genus, *Isepeolus*) occurs from temperate Brazil to Argentina and Chile.

The remaining tribes of Nomadinae are the mostly small "pasitine" bees, as a whole better represented in the Old World than in the New World. Their relationships to other Nomadinae are not clear but recent studies support their inclusion in that subfamily (J. G. Rozen, in litt.).

The tribe Caenoprosopidini contains a single genus (*Caenoprosopis*) and species found from southern Brazil to Argentina.

The Neolarrini and Townsendiellini are Nearctic, largely restricted to xeric areas. Only three genera and subgenera are involved. The Ammobatini are most diverse in Africa (6 genera) including Madagascar (which has an endemic genus as well as an African genus) but three genera range into or are largely restricted to the Palearctic region and one (*Oreopasites*) is found in the western United States.

The tribes Holcopasitini and Biastini each contains two genera, one Nearctic, one Palearctic. The tribe Ammobatoidini contains a single genus which is Palearctic.

The last anthophorid subfamily is the Xylocopinae. While a few species of the subfamily occur in Mediterranean climates or even desertic areas, the only groups limited to such areas are *Proxycopa* and *Manuelia*. The tribe Xylocopini contains the large carpenter bees, most of which nest in wood or coarse stems. It is primarily tropical and subtropical in both hemispheres, with a few groups and species penetrating well into the temperate zones. The diversity of the group is greatest in the Eastern Hemisphere. There is a ground-nesting Mediterranean to central Asian genus (*Proxycopa*) and an Australian genus (*Lestis*) in addition to the widespread *Xylocopa*.

The latter genus has been much subdivided. It is abundant in the moist tropical as well as in drier tropical and subtropical regions. In the Americas there are 17 subgenera. Most are Neotropical, being especially numerous in the area of southern Brazil to Argentina; two primarily Neotropical subgenera reach the southern United States and one of them is in the Antilles also. Two of the 17 subgenera are Nearctic, extending into the northern Neotropics, and one is Mesamerican. None occurs in the Araucanian region. There is no special abundance of *Xylocopa* in the Madrean area and no species are restricted to that area.

In the Old World there are 31 subgenera. Fifteen of these occur in Africa, a few of them also being in India and southeast Asia, and one, *Koptortosoma*, ranges from Africa to the Philippines and through Indonesia to New Guinea and Australia. There are no other groups of *Xylocopa* in Australia. Unusual for bees, *Xylocopa* has 11 subgenera restricted to the Oriental Region, some found only or principally in southeast Asia and three restricted to Indonesian islands. Three subgenera are primarily Palearctic and several others enter the Palearctic region slightly in India, China, or the Mediterranean basin.

No subgenus occurs both in the Americas and in the Old World. However, there are some relationships that suggest several dispersals perhaps across the North Pacific. Thus the Palearctic *Xylocopa* s. str. resembles the Nearctic *Xylocopoides*, the Chinese *Mimoxycopa* resembles *Stenoxycopa* which ranges from Argentina to Arizona, and the Palearctic (and African) *Rhysoxycopa* resembles *Notoxycopa* of the western United States (and south to Colombia). The other major disjunctions are those which occur in the African-Oriental subgenera which skip from Africa to India. The Malagasy *Prosopoxycopa* is related to the Oriental *Zonohirsuta*, not to African subgenera.

The other tribe of the subfamily Xylocopinae is the Ceratinini, or small carpenter bees. The genus *Manuelia* contains three species, each very different from the others, perhaps at a generic or subgeneric level, and all restricted to the Araucanian region. This is probably an archaic genus; it has no close relatives elsewhere. *Ceratina* is a large genus, abundant on all continents except Australia which has only one species which is similar to forms found in India and intervening regions. The genus has been divided into a dozen or more subgenera (Michener, 1954; van der Vecht, 1952) but as no worldwide study has yet been made, the biogeography of the subgenera is not clear. In particular, the rich African fauna has received little classificatory attention. There is no evidence of major disjunctions, nor of close relationships between groups of the southern continents. As with *Xylocopa* and unlike most groups of bees, there are a number

of Oriental groups (*Chloroceratina*, *Catoceratina*, *Lioceratina*, *Xanthoceratina*, *Ceratinidia*, *Pithitis*) most of them restricted to southeast Asia and major continental islands. *Ceratinidia* and *Pithitis* range across Indonesia to New Guinea and the latter has a single species in Africa. While its dispersal southeast from Indonesia is very limited (2 species, one reaching the Solomon Islands, the other reaching middle latitudes in eastern Australia), *Ceratina* extends far across the Pacific farther north, having an endemic species in Micronesia (Krombein, 1950). *Ceratina* includes about six subgenera in the Americas, only one of them primarily Nearctic, the others either restricted to or best developed in the Neotropical region. There are species in the Antilles.

The remaining Ceratinini constitute a group commonly called the allodapine bees (Michener, 1977). Their center of abundance and diversity is Africa, where there are ten genera and subgenera. Six of these taxa are restricted to southern Africa, which thus has greater diversity than any other area (Michener, 1975). One major African genus, *Braunsapis*, also occurs in southern Asia and east as far as Taiwan, the Philippines, Solomon Islands, and the northern half of Australia. Another extends beyond Africa only to the Arabian Peninsula. There is also a monotypic genus (*Exoneuridia*) restricted to Asia Minor. It is the only north temperate allodapine genus, although *Braunsapis* enters temperate climates marginally in Asia. The African genera *Macrogalea* and *Halterapis* as well as *Braunsapis* are found on Madagascar, where there is also another genus, *Effrac-tapis*, derived from *Braunsapis*.

Four additional genera and subgenera, *Exoneura* and its relatives, occur in Australia. All are restricted to temperate parts of the continent and one of them reaches Tasmania.

Those allodapines that have the largest number of ancestral characters (characters in common with *Ceratina*) are African. The group may well have originated there and spread thence over the rest of the Old World tropical and south temperate regions. *Braunsapis* presumably arrived in Australia from the north by way of the islands, among which it has shown a good dispersal ability. The way has been open, more or less as at present, for 15 m.y. The *Exoneura* group of genera presumably reached Australia earlier, and either was to begin with or became, adapted to temperate climates.

To summarize for the Anthophoridae, it seems likely that the initial radiation was in South America, probably after that continent was more or less isolated. This radiation involved the Exomalopsini and various groups probably derived from it like the Tetrapediini, Melitomini, Eucerinodini, Canephorulini, Eucerini, Centridini, Ctenioschelini, Rathymini, as well as the subfamily Nomadinae. Of these only the Exomalopsini-Ancylini, perhaps with the Pararhophitini, the Eucerini, and the Nomadinae reached the Old World, principally the Palearctic, probably via North America, but several of the other groups penetrated into North America. The Anthophorini and Melectini are predominantly Old World groups whose relationships to the New World groups are not clear. They are probably ultimately derivatives of Exomalopsini or similar bees. The radiation of the Xylocopinae has been primarily tropical, in both eastern and western hemispheres. The most primitive genus of Xylocopini, however, is the Mediterranean to central Asian

*Proxycopa*. Useful speculation as to areas of origin and initial radiation for both Xylocopini and Ceratinini seems premature.

#### APIDAE

This family, which includes all the highly social bees as well as others, has, for that reason and because of the apparently specialized pollen-carrying corbicula, usually been considered as the most specialized of the long-tongued bees. However, the distribution of what is presumably the oldest group (Meliponinae, the sister group of all the other Apidae according to Winston & Michener, 1977) exhibits discontinuities that may indicate greater antiquity than for surviving groups of other long-tongued families except the Fideliidae.

The Meliponinae or stingless honeybees are pantropical, richly represented in the wet tropics and usually less abundant in other tropical areas, extending into the temperate zone in the southern continents but not or scarcely in the northern ones. Before general acceptance of continental drift, I believed that the intercontinental tropical discontinuities of Meliponinae, different from any other bee distributions, indicated an ability to traverse oceans rarely as nests in hollow trunks. Their food stores and known ability to survive imprisonment in their nests made this hypothesis seem reasonable. However, the Meliponinae seem actually to be poor at dispersal across water. In spite of a rich continental fauna there is only one extant Antillean species and it is the same as the principal domesticated species of *Melipona* in Yucatán. It is likely that it was carried to the Antilles by primitive man. There are few Malagasy species, all closely related to African forms of the genus *Trigona*, subgenus *Hypotrigona*. Only in the east Asian and Indonesian area is there evidence of considerable island-hopping, for species of the subgenus *Tetragona* are found in the Philippines and throughout Indonesia and beyond to the Solomon Islands and Australia. Most of the *Tetragona* species east of the islands recently joined with Asia belong to a single small group of closely allied species called by Moure (1961) *Tetragonula*. Perhaps this group possesses some attributes that make over-water transport more likely than for other groups. Krombein (1950) attributes the presence of two species in Micronesia to man. In any event, it now seems probable that for most Meliponinae, oceans have not been traversable; the disjunct distributions are probably explicable in part on the basis of plate tectonics.

The Meliponinae have been much subdivided (Moure, 1961) but the 19 genera and subgenera recognized by Wille (in preparation) are more instructive than finer subdivisions for biogeographical studies. There exist three main groups: *Melipona* in tropical America (Argentina to Mexico), *Meliponula* (in spite of its name not closely related to *Melipona*) with a single widespread tropical African species, and the group of *Trigona* and its allies (including *Lestrimelitta* and *Dactylurina*) in all tropical continental areas. The latter group is by far most diverse in tropical America, where there are 14 genera and subgenera. Among the American forms are the subgenera *Trigona* s. str., *Trigonisca*, *Tetragona*, and *Plebeia* of *Trigona*, all with many species, and the genus *Lestrimelitta* containing two species of robber bees that never visit flowers but forage in the nests of other

Meliponinae. All American subgenera of *Trigona*, as well as *Lestrimelitta*, are rather widespread, at least from Brazil to Costa Rica, and most from northern Argentina to Mexico. In southern Brazil and adjacent countries there are three or four distinctive species or species groups of *Trigona* not found elsewhere. No such unusual forms occur near the northern limit of the stingless bees' range in Mexico. No meliponines reach the Araucanian area, and no members of the *Trigona* group now occur in the Antilles, although as indicated elsewhere, fossils of the subgenus *Hypotrigona* have been found in Hispaniola.

The *Trigona*-group of Africa comprises only five genera and subgenera. Two of these, *Meliplebeia* and *Axestotrigona*, are strictly African. The others show noteworthy similarities to Neotropical forms. *Hypotrigona* of Africa is closely related to the Neotropical *Trigonisca*. There are several species of *Plebeia* differing from those of the Neotropics in having a larger and presumably ancestral (but nonfunctional for stinging) sting apparatus. There are no *Tetragona* species in Africa but a single species placed in the separate genus *Dactylurina* is nothing but an unusual *Tetragona*. Finally, the African robber bees are placed in *Cleptotrigona*, which may be related to the American robber genus *Lestrimelitta* or may be independently derived from flower-visiting *Trigona* (*Hypotrigona*) species in Africa.

The *Trigona* of southern Asia, although much more numerous in species and individuals, especially in southeast Asia, than in Africa, all belong to three subgenera. One is tentatively considered as *Hypotrigona*, the same subgenus as those of Africa. Another is *Lepidotrigona*, found only from India to Java and Borneo. The third, a large group in the Oriental area, is *Tetragona*. It contains numerous subgroups and many species, and ranges from Sri Lanka and India to Borneo and Java with one species group extending onward to the Philippines, Solomon Islands, and south to the northern half of Australia. None of the Oriental species groups is the same as those of the Americas, but the presence in both continents of forms of *Tetragona* with and without sericeous hind basitarsal areas suggests at least two intercontinental dispersals. Repeated detailed studies (Wille, 1977) show no consistent differences between Oriental and Neotropical groups of *Tetragona*.

Finally, in the north half of Australia and in New Guinea, in addition to the *Tetragona* mentioned above, there exist species of the subgenus *Plebeia* similar to those of the Americas, lacking the primitive features of the African *Plebeia* species.

The *Trigona* species from the Eocene Baltic Amber cannot be placed in any of the modern subgenera and apparently constitutes an undescribed subgenus. *Trigona silicea* from Oligomiocene amber in Chiapas, Mexico, is a member of the small Neotropical subgenus *Nogueirapis*, a relative of the subgenus *Plebeia*. Thus at least the more primitive extant groups were in modern form by the beginning of the Miocene. The most interesting fossil is *Trigona dominicana* from Oligocene (?) amber of the Dominican Republic (Wille & Chandler, 1964). It demonstrates that the *Trigona*-group once occurred in the Greater Antilles, although now extinct there. Moreover, it is a *Hypotrigona*, a subgenus not now found in the Americas although present in Africa, Madagascar, and southeast Asia.

Since at least three transatlantic dispersals would be necessary to explain the

disjunctions described above (for *Plebeia*, *Tetragona*, and *Hypotrigona-Trigona*), fortuitous transport seems unlikely. It is more likely that the principal subgenera of *Trigona* originated in the middle or upper Cretaceous when Africa and South America were joined or not yet widely separated in tropical latitudes (see Förster, 1978).

The subfamily Bombinae contains two very different tribes. The Euglossini consists of about eight genera and subgenera, all found in tropical America. The major genera (*Euglossa*, *Eulaema*, *Euplusia*) range from northern Argentina to Mexico; others, especially *Aglae*, are limited to the Amazon or similar forests. One species of *Euglossa* occurs in Jamaica; otherwise the tribe is absent in the Antilles.

The tribe Bombini consists of two genera, *Bombus* and *Psithyrus*, the latter parasitic in nests of the former. The tribe is primarily holarctic, and most abundant in cool temperate zones, but species of *Bombus* range essentially as far north as there is land in the arctic as well as to Tierra del Fuego in the south, thus into colder climates than are inhabited by any other bees.

*Psithyrus* is restricted to the Holarctic region. *Bombus* is divided into 35 subgenera (Richards, 1968). Of these five are Holarctic and 17 Palearctic, so that 22 occur in the Palearctic region, the area of greatest diversity. By contrast, there are only five Nearctic subgenera (one of them also Neotropical), making a total of 10 in the Nearctic region. Five subgenera occur in South America, mostly in Andean and southern regions, although two species exist in the Amazon Valley. One Holarctic subgenus extends into southeast Asia and there are three other Oriental subgenera, all montane, one extending as far southeast as the mountains of Java. The genus is probably absent in sub-saharan Africa. A single queen of an American subgenus has been described from Guinea (Tkalců, 1966), but it is likely to represent an introduced or possibly mislabeled individual.

The subfamily Apinae contains only the genus *Apis*. Prior to dispersal of *A. mellifera* by man, the genus was restricted to the Oriental, Palearctic, and African regions. The greatest diversity is in the Oriental region. While it occurs in Taiwan and the Philippines, the genus does not reach New Guinea or Australia. One species, *A. cerana*, ranges from southern Asia to Palearctic China and Japan. Another, *A. mellifera*, ranges from western Asia throughout Africa (including Madagascar) to the Cape and north in Europe as far as southern Norway. Except for these two species, the genus is tropical and subtropical, and Oriental. Obvious members of the genus occurred, however, in Europe in the Oligocene (Zeuner & Manning, 1976), as did the extinct apine genus, *Electrapis*, in the Eocene.

To summarize for the Apidae, the Meliponinae are apparently an ancient tropical group that arose and radiated in the former West Gondwanaland when Africa and South America were much closer than at present. The subfamily is now best represented in South America. The Bombinae may have had a similar origin, for the Euglossini are strictly Neotropical, but the Bombini entered cool temperate climates and radiated primarily in the cool Palearctic region. The origin of the Apinae is obscure, but it is now centered in the Oriental region, occurring also in the African and Palearctic areas, and was in the last mentioned as early as late Eocene.

## DISJUNCTIONS

The distributions of most bee taxa are not disjunct or, if so, are limited to neighboring continents and could have been attained with the continents in their present positions. Some taxa are found in most or all continents and even many islands, and obviously have considerable potential for traversing major water barriers. Probably the dispersal of some such groups preceded the present arrangement of the continents, but when we lack knowledge of the cladistics within a taxon (e.g., of subgenera within a genus), no conclusions can be drawn as to the time and manner of the major dispersal. Numerous taxa, by occurring on both sides of a major physiogeographic or climatic barrier, provide some information on their antiquity or dispersal ability.

The very many Holarctic taxa are all disjunct. Those that occur in boreal environments may be scarcely so, however, and there are a few Holarctic species (in *Andrena*, *Halictus*, *Osmia*, *Formicapis*, *Clisodon*, *Bombus*) that presumably crossed the Bering Strait area sufficiently recently that obvious or species-level differentiation of North American and Eurasian populations has not occurred. Most bees, however, require warmer climates than those now found in the Bering Strait area; intercontinental dispersal was therefore older and Eurasian and North American populations are mostly at least specifically distinct.

Some taxa or groups found in both northern continents and not occurring north of the more or less warm temperate zone are the following: *Nomia* (2 groups), *Panurginus*, *Macropis*, *Diceratosmia*, *Chalcosmia*, *Chelostoma*, *Heriades*, *Trachusa*, *Anthidiellum*, *Xenoglossodes*, *Melecta*, *Holcopasitini*, *Biastini*, *Xylocopa-Xylocopoides*, *Mimoxylocopa-Stenoxylocopa*, *Rhysoxylocopa-Notoxylocopa*. Probably most of these groups traversed the Bering Strait area. Restriction of several of the groups (*Chelostoma*, *Trachusa*, *Biastini*, *Notoxylocopa*) in America to the west suggests this route. Others, such as *Nomia* and *Melecta*, are principally western in North America. Certain of the forms listed, however, are largely eastern in their American distributions (*Macropis*, *Diceratosmia*). This limitation might result from the current climate, but also suggests dispersal across the north Atlantic, a route which was open for plants throughout the Tertiary (Raven & Axelrod, 1974), although becoming less and less practical as North America and Europe moved apart.

Many organisms inhabit Mediterranean and desertic climates of both North and South America and are absent from the intervening tropics. These amphitropical distributions have long been a subject of interest (Raven, 1963, 1972; Raven & Axelrod, 1974). Among the bees, none involves specifically the Californian area of Mediterranean climate, nor are there polar (boreal) amphitropical bees. In North America most amphitropical bees are primarily Sonoran and Chihuahuan desertic elements, although *Caupolicana*, *Protandrena*, and *Ptilothrix* each has an eastern North American species or two. Other amphitropical taxa (Andreninae, Dufoureae, and *Calliopsis* and allies) are wide ranging in North America. In South America, amphitropical bees occur either in the Argentina-southern Brazilian area, often in its more xeric parts, or in the Araucanian region. The following lists of amphitropical taxa show that only *Calliopsis* and its relatives



and *Protandrena-Psaenythia* occur in both. (*Protandrena* and *Psaenythia* are listed in this paragraph by virtue of their close relationship to one another; each is restricted to its continent but they constitute an amphitropical group.)

Amphitropical groups occurring in Argentina-southern Brazil: *Eulonchopria*, *Zikanapis*, *Protoxaea* s. l., *Protandrena-Psaenythia*, *Calliopsis* and relatives, *Dasiapis*, *Ptilothrix*, *Martinapis*, *Protepeolus*.

Amphitropical groups occurring in the Araucanian region: *Caupolicana* s. str., *Dufoureaeinae*, *Andreninae*, *Protandrena-Psaenythia*, *Calliopsis* and relatives, *Xerocentris*.

Certain other tentatively amphitropical or almost amphitropical groups are listed in the preceding section.

Dispersal between the savanna, grasslands, macchia, and deserts of South America and similar arid environments of North America must have been greatly facilitated by aridity in the tropics during the Pleistocene. In some cases (especially the *Dufoureaeinae* and *Andreninae*), however, the South American forms are quite different from any North American ones and dispersal must have been much earlier. As there is no evidence for an arid corridor during the Tertiary (or at any other time), long distance dispersal probably accounts for such distributions, perhaps facilitated by local xeric areas as suggested by Michener (1954). The elevation of the Andes progressively increased the possibility of intercontinental dispersal by creating cool or arid habitats near the equator. There is an alternative to long distance dispersal, however. From time to time in its history a xeric-adapted genus may give rise to a species able to exist in mesic or humid habitats. For example, *Ashmeadiella*, a generally xeric-adapted genus, has one species that ranges eastward in North America as far as Indiana and Georgia and another that occurs from North Carolina to Florida. Should such a species reach another xeric area, it might well speciate there, and if it then disappeared in the intervening mesic area, one could have a cluster of species in each xeric area and a problem in explaining how the genus traversed the mesic area.

The direction in which amphitropical groups spread is sometimes not obvious. However, it is probable that *Penapis* (*Dufoureaeinae*) and *Euherbstia* and *Orphana* (*Andreninae*) originated in the north while *Eulonchopria*, *Zikanapis*, *Caupolicana* and probably most of the rest originated in the south.

In the Old World, many tropical groups occur in Africa, and then again from Sri Lanka and India eastward across southern Asia, often with little differentiation between forms in the two areas. A more humid (not wet tropical but savanna) climate across the Arabian peninsula, southern Iran, and west Pakistan would connect or nearly connect these areas for the bees concerned, even with the continents in their present positions. Since more humid conditions undoubtedly existed in this area in the not very distant past, this disjunction, like that for cool temperate forms across Bering Strait, is easy to understand. Some of the taxa involved are *Thrinchostoma*, *Pachyhalictus*, *Ctenoplectra*, *Creightonella*, two or more subgenera of *Chalicodoma*, various subgenera of *Xylocopa*, and *Braunsapis*. Certain others may have crossed from Africa to southern India directly or via islands, and have not extended farther eastward. Such forms are *Eupetersia* and *Eucara*. There is nothing to indicate that any aspects of modern bee distribution

in the Indian Ocean area depend upon movements of Madagascar or India. Any bees which were in India when it moved across the Indian Ocean are lost or have dispersed widely (possibly like *Hylaeus*) and become unrecognizable as such.

Most of the taxa having an African-Oriental distribution have their centers of diversity in Africa. The reverse is true for *Pachyhalictus*, *Pithitis*, *Apis* (the last two with only 1 African species each), and for *Hoplonomia* and the *Prosopoxycopa-Zonohirsuta* group of *Xylocopa*, which reach Madagascar but not Africa proper.

For some groups the island-filled sea between Asia and Australia is only a partial barrier. Before the Miocene (about 15 m.y. BP) the sea was broader, probably without large islands, and accordingly was an effective barrier. Various groups of bees occur both in Asia and Australia, as well as intervening islands. Such distribution is found in *Homalictus* (probably an old Australian genus that spread to Asia) and in *Lasioglossum* s. l., *Sphecodes*, *Nomioides*, various subgenera of *Nomia* and of *Chalicodoma*, *Amegilla*, *Braunsapis*, *Tetragona*, and others (all of which appear to have spread from Asia to Australia). In some cases Asiatic and Australian species are very similar, indicating recent spread across the ocean barriers.

The remaining disjunctions to be discussed are probably all old, perhaps resulting from or exaggerated by continental movements that occurred during and since the Cretaceous. The bees involved (with the possible exception of *Chelostomoides-Hackeriapis* and the Meliponinae) seem to be archaic types, and the taxa may have been parts of the initial rapid radiation of the bees. Except for the Meliponinae, all the taxa discussed below are largely inhabitants of xeric areas; the Fideliidae and the *Hesperapis* group are limited to such areas. Thus the importance of xeric environments as habitats for primitive bees is reemphasized.

The Paracolletini are found principally in temperate parts of Australia, South America, and Africa and the Fideliidae in desertic parts of Chile and South Africa. Dispersal between Australia and South America through cool temperate Antarctica would have been possible as recently as the beginning of the Oligocene (38 m.y. BP). This route could perhaps have been traversed by the paracolletines. Connections to Africa were disrupted earlier; by the end of the Cretaceous, while relatively narrow seas separated tropical Africa and South America, temperate parts of these continents were already well separated. Thus the Fideliidae and perhaps the Paracolletini may have originated as long ago as the Upper Cretaceous. (As indicated elsewhere, however, long distance transoceanic dispersal could explain the Afro-Australian or Afro-American disjunctions of Paracolletini and Fideliidae, respectively.)

Dispersal among xeric areas outside the southern hemisphere also presents difficult problems. The primarily Australian-North American distribution of the *Hackeriapis-Chelostomoides* group of *Chalicodoma* has been discussed elsewhere. (*Hackeriapis* is Australian, north to New Guinea savannas; *Chelostomoides* is North American, especially Madrean, south to Colombia.) Long distance dispersal seems unlikely from Australia to North America. The Bering Straits would seem a likely route, but if it were used, why is the nearest relative of

*Chelostomoides* in Australia instead of in Asia? Alternatively, dispersal from Australia to South America through cool temperate Antarctica would have been possible in the Paleogene, but if this route were used, what happened to the group in most of South America, some of which is climatically and vegetationally so similar to the desertic areas of North America where *Chelostomoides* is abundant and diversified?

The *Hesperapis* group of genera (South Africa, Central Asia, and the Madrean and adjacent areas) also occurs in deserts of both the Northern and Southern Hemispheres. It may have originated in arid parts of Africa, as suggested by the presence of related melittids there, and during dry epochs extended to the Mediterranean-Central Asian arid zone. Certain other bees have such distributions, and *Poecilomelitta* ranges from arid southern Africa to Iran, without entering the Mediterranean basin. The unusual feature of the *Hesperapis* group's distribution in the Old World is its absence between Central Asia and South Africa. It probably became extinct between these areas; there is no need to postulate long distance dispersal. The problem is, how did it get to the New World? The Exomalopsini-Ancylini may have spread from arid parts of North or South America to the Mediterranean region. The Old World forms are mostly in arid areas, as are some Exomalopsini. Moreover, the similarities of such bees as desert *Hoplitis* (and related genera) and desert *Anthophora* (subgenus *Micranthophora*) of the Madrean area to those of the Mediterranean-Central Asian area may not be convergent, but may possibly result instead from common ancestry. Further studies are needed to determine the cladistic relationships. In any case, at least some bees moved between the Old World and New World dry areas. Raven & Axelrod (1974) suggest that eastern North America and western Europe were in latitudes suitable to warm, seasonally dry climates in late Cretaceous and early Eocene, and were separated by only moderately broad seas. If so, bees of dry areas could have been exchanged more readily than under present conditions, but probably only by long distance dispersal as emphasized by Raven (1972).

The disjunctions noted previously for Meliponinae are unique among bees in that they involve a group characteristic of the moist tropics, and except for one subgroup, with minimal ability to cross water. The disjunctions are indicated as follows:

*Plebeia*—American tropics, Africa, Australia and New Guinea.

*Tetragona*—American tropics, Africa (related *Dactylurina*), Oriental region to Australia.

*Hypotrigona-Trigonisca*—American tropics, Africa, Oriental region.

*Lestrimelitta* (if monophyletic)—American tropics, Africa.

The genus *Trigona* was present in Europe in the Eocene (Baltic amber) (Kelner-Pillault, 1970); it probably dates from before that time, and some modern subgenera such as *Plebeia* from not much later. Raven & Axelrod (1974) indicate that Madagascar and India might have served as a subtropical migration route between Africa and Australia until near the end of the Cretaceous (see their Fig. 2). If *Plebeia*, which is among the most primitive Meliponinae, reached Australia at that time and disappeared from India as it became dry during its

movement toward Asia, the absence of *Plebeia* in Asia and its presence in Africa, Australia and New Guinea could be explained. The South American-African connection was severed in earlier Upper Cretaceous, suggesting an antiquity for *Plebeia* of 65 to 100 m.y., that is, an origin for the subgenus in the Upper Cretaceous. This seems unlikely in view of the probable time of origin of the bees; dispersal across a narrow Atlantic seems more likely; in tropical latitudes the Atlantic remained narrow for a long time (Förster, 1978). Perhaps *Tetragona*'s occurrence both in the Old World and in the Neotropics can be explained in the same way. *Tetragona* may have spread in the Old World relatively recently, becoming extinct, except for the derived *Dactylurina*, with drying and elevation in Africa. *Hypotrigona-Trigonisca* is a primitive group whose trans-Atlantic dispersal could be explained as for *Plebeia*.

#### COMPARISON OF FAUNAL REGIONS

A rough comparison of bees in faunal regions can be obtained by comparing the columns in Table 3. The last row in that table gives the numbers of tribes, subfamilies, and families found in each faunal region. This is one measure of faunal richness or poverty. Another is the number of genera and subgenera found in each region, as follows:

Australian—127	Neotropical—315
African—175	Nearctic—260
Oriental—89	Palaearctic—243

The above figures are based on numbers which for different groups in different areas are mere estimates. Thus for a genus that has been well revised and divided into meaningful subgenera in certain continents, I have estimated (or made a guess at) the probable number of subgenera in other continents where appropriate studies have not been made. Moreover, I have omitted some genera or subgenera that enter a certain area only marginally. For example, the widespread Neotropical genus *Pseudaugochloropsis* is not counted in the Nearctic region although it has been taken near Brownsville, Texas.

In the following paragraphs attributes of the fauna of each faunal area are described. To avoid duplication, I have not usually repeated below, but have merely referred to, the information on disjunct distributions contained in the preceding section. Ideally, for any area, one ought to be able to indicate which taxa originated in that area, and which entered it, and when, from which other areas. In the almost complete absence of a useful fossil record, one is largely dependent upon present distributions and surmises as to past climates and continental connections. I have made this section brief by omitting many purely speculative considerations.

*Australia* is the only continent where a high percentage of the taxa (64% of the genera and subgenera, nearly half of the species, Michener, 1965a) belong to the primitive family Colletidae. Presumably this results from the long isolation of the continent, from the time of its separation from the rest of Gondwanaland at the end of the Eocene until its present broken connection with Asia devel-

oped in late Miocene. It probably preserves something resembling the temperate Gondwanaland bee fauna, infiltrated by various other types.

Aside from the colletids, only *Hackeriapis* in the Megachilini (relatives in North America) and *Plebeia* in the Meliponinae (also in Africa and the Neotropics) among Australian bees show major disjunctions. Other groups all could have reached Australia from Asia at various times during Australia's approach to that continent. Ancestors of the *Exoneura* group (Ceratinini) and of some halictids, especially *Homalictus* and *Austronomia*, however, probably arrived early, possibly via southern connections. Thus all these groups also could have been part of the Gondwanaland bee fauna. Absence in South America of bees related to the halictids and Ceratinini mentioned above may suggest that they were early transoceanic arrivals. It must be remembered, however, that Australia and South America were never in contact but were joined by Antarctica, a large continent whose effectiveness as a faunal bridge was limited in the early Tertiary to forms able to tolerate cool temperate climates. For warm-temperate organisms this bridge probably failed about 100 m.y. BP, before the middle of the Upper Cretaceous.

Most of the large Australian bee fauna inhabits the dry temperate region, and is dependent on Myrtaceae for pollen and nectar (Michener, 1965a). Australia is the only continent where one family of plants has a pre-eminent position as a food source for bees. These bees are not well represented, although present, in cool temperate areas; only 20 genera and subgenera occur in Tasmania.

The typical Australian groups are surprisingly poorly represented in the Australian rainforests, in New Guinea and nearby islands, and even in the dry savannas of tropical northern Australia. Various Australian groups do occur, however, in northern Australia and New Guinea, and a few (*Palaeorhiza*, *Homalictus* and certain subgenera of *Nomia*) are unusually developed in New Guinea. A few taxa from Asia enter this region (New Guinea and northernmost Australia) but not temperate Australia; *Pachyhalictus*, *Ctenoplectra*, *Chelostomoda*, and *Pycnanthidium* are examples. In fact, if one ignores the Australian elements, the fauna of northern Australia, New Guinea, and the Solomon Islands is a depauperate extension of the Oriental fauna, which is itself a depauperate extension of the African fauna. Thus there is a single paleotropical bee fauna, richest in Africa and progressively reduced to the east.

*New Zealand and New Caledonia* have the smallest bee faunas of any substantial land areas of the world. New Zealand has only four native genera and subgenera; species are also few. These islands have no unusual genera or higher categories that might have been there since these land masses were isolated in the Upper Cretaceous, 80 m.y. BP. If these lands had bees at that time, they must now be extinct. The few bees on the islands today are all congeneric with Australian forms, and all but a few New Zealand species of *Leioproctus* are in the same subgenera as Australian species. Thus the entire fauna appears to have arrived relatively recently over the water.

*Sub-Saharan Africa* (for simplicity usually called "Africa" in this paper) has a rather rich tropical bee fauna. Nomiinae, Megachilini, various halictids, Xylocopini, and Ceratinini are especially well represented, and for Nomiinae, Mega-

chilini, Xylocopini, Ceratinini, Ammobatini and Ctenoplectrinae, this is the center of diversity. Some large groups of Halictini such as *Zonalictus* and *Thrinchostoma* are either restricted to or centered in tropical Africa. Some or all of the groups listed above may have originated in Africa. There is no evidence that they originated prior to the break up of Gondwanaland, although the representation of the Nomiinae, Megachilini, Ceratinini (*Exoneura* and relatives) and also the subgenus *Plebeia* in the Meliponinae in Australia suggests that these groups might date to that time. More likely most of these groups merely crossed narrower oceans than those that now separate these continents. The good representation of *Xylocopa* and *Ceratina* in South America might suggest the same thing.

Africa was connected to or very near Eurasia until the Paleocene (about 63 m.y. BP) and again since the Miocene (about 25 m.y. BP). Thus faunal interchange with the Palearctic (which region now includes the north African coast) has long been possible, and there is no good evidence as to which tropical African groups originated there and which came from Eurasia (southern European parts of which once had tropical climates). The continental limits have not coincided with the climatic limits and plants and insects have, to a certain degree, been able to ignore the former.

Africa is surprisingly lacking, so far as known, in xeric-adapted forms along the southern margin of the Sahara, but various tropical genera exist in the east African savanna and into Ethiopia and Somalia. Some primarily tropical groups like Nomiinae and *Xylocopa* are represented not only in the marginally tropical areas but also in the Mediterranean basin and southern Europe.

The tropical African forest fauna is sparse compared to that of South America, possibly because of the more severe results of tropical aridity, as well as because of lack of a large south temperate source area and the persistent oceanic, savanna, or desert barrier to the north. Among bees, there is no evidence of widespread extinctions in Africa. There are no groups of bees found in South America and Madagascar or South America and southeast Asia, but absent in Africa, a well known distributional pattern in plants (Raven & Axelrod, 1974). This is not surprising considering that bees generally do well in dry areas, and the only partial exception is the subgenus *Tetragona* of the Meliponinae, represented in Africa only by a specialized derivative, *Dactylurina*. The meliponines, unlike most bees, are primarily insects of tropical moist forests. The meliponine fauna of Africa is the smallest of any major tropical area, although some of the species are in some features the most primitive extant members of the subfamily. Certain Palearctic forms such as *Andrena*, the Dufoureae, the subgenus *Seladonia* in the Halictini, some megachilid taxa including *Hoplitis*, and probably the African groups of Panurginae, range south through east Africa and enrich not only the equatorial African fauna but that of the Cape region.

Other continents, of course, also have contributed to or received elements from tropical Africa. As noted below in the discussion of the Oriental region, a few taxa centered in that area enrich the African fauna, although for most bee groups Africa has the richer and the Orient the more depauperate representation. South America and Australia show special relationships to tropical Africa only in the Meliponinae.

The *Cape region of South Africa*, including most of Cape Province, has a distinctive bee fauna, most elements of which also occur in the more mesic parts of southern Africa like Natal. This fauna lacks many elements of the tropical African fauna (although including some, such as the allodapines *Allodape* and *Braunsapis* and the halictid genus *Zonalictus*), and it is characterized by a number of other groups, some of them presumably archaic. The Melittinae and Dasypodinae are better represented and more diverse in southern Africa than elsewhere and the following are restricted to that region: the paracolletines *Scrapter* and *Parapolyglossa*, the fideliids *Fidelia* and *Parafidelia*, the halictid *Patellapis*, an undescribed genus of Hylaeinae, and the allodapines *Halterapis* and *Allodapula*. As noted elsewhere, some of these taxa probably had Gondwanaland origins and date to early apoid radiation. Thus the paracolletines are otherwise Australian and temperate South American, the Fideliidae are otherwise Araucanian, and the Hylaeinae may suggest an Australian connection. Certain forms of Palearctic origin, such as *Andrena* and the Dufoureinae, as noted above, also occur in the Cape region, but none has speciated to produce a large south temperate group or complex in Africa.

While the Cape region has a rich and interesting bee fauna, there is no counterpart to its enormous flora (Axelrod & Raven, 1977). Bee species are seemingly less numerous on the Cape Peninsula than somewhat to the interior, and there is none of the fantastic speciation that has occurred in plant genera, e.g., *Erica*.

*Madagascar* has a few distinct genera such as *Parathrincostruma* and *Effractapis*. Its fauna has been poorly studied and there are probably others to be recognized. However, there is no evidence of archaic types that might have been isolated there when Madagascar separated from Africa in the Upper Cretaceous, nor is there evidence of survivors there of formerly widespread taxa that may have become extinct in Africa. The fauna has been accumulated from repeated transoceanic dispersals, mostly from Africa but with a few taxa (e.g., *Hoplonomia*, *Prosopoxylocopa*) from the Oriental region.

The *Oriental faunal region* includes areas of both Gondwanaland (India) and Laurasian origin, and for purposes of bees, should perhaps be considered to extend as far east as New Guinea, which is also largely of Gondwanaland origin. The Oriental region has the poorest tropical bee fauna in the world (except that of Northern Australia and New Guinea) in spite of the fact that it is the richest area in the world in endemic primitive angiosperms. To a major extent it is inhabited by a depauperate African bee fauna. The section on DISJUNCTIONS lists some of the African taxa that also range from India eastward across southern Asia and indicates how they probably reached Asia from Africa. Some taxa, such as *Eupetersia* and *Eucara*, only reach India, while most (*Thrincostruma*, various Nomiinae, *Ctenoplectra*, *Creightonella*, *Braunsapis* and various subgenera of *Megachile*, *Chalicodoma*, and *Xylocopa*) extend eastward at least to the Asiatic continental islands and some beyond, as far as New Guinea, the Solomon Islands, and even northern Australia. Perhaps the periodic arid epochs have benefited the tropics elsewhere (especially in the Americas) as bee habitats and led to much speciation and evolution on tropical faunas, whereas the Oriental faunal region, relatively small in size, has not experienced much aridity except in India, where

Palaearctic bees rather than derived Oriental ones have occupied the dry zones. The Oriental area does have a few distinctive subgenera or genera, restricted to or at least centered in the Oriental region. These include *Pachyhalictus*, *Hoplonomia*, certain small anthidiine taxa, subgenera of *Xylocopa* and *Ceratina*, *Thygatina*, *Elaphropoda*, *Protomelissa*, *Lepidotrigona*, and *Apis*.

The Oriental fauna is enriched by a few groups from Australia and a larger number from the Palaearctic. Groups centered in Australia that have probably dispersed northwestward are *Homalictus* and *Austronomia*. Some of the primarily Palaearctic taxa are the same taxa that enter Africa, but most invaded the tropics separately in Africa and in Asia. Groups involved include *Halictus* s. str. and *Seladonia*, *Sphecodes*, *Systropha*, *Andrena*, *Hoplitis*, *Nomada*, and *Bombus*.

The tropical part of the *Neotropical region* is characterized by the abundance of Meliponinae, including the genus *Melipona*. Disjunct distributions and poor dispersal abilities suggest that meliponines may have originated before the fragments of Gondwanaland became widely separated (see also Moure, 1951). The large group of genera of augochlorine halictids is also abundant in the tropics and must be ancient, considering its size and diversity. Its absence in Africa and Australia suggests that it postdates the breakup of Gondwanaland, as could be true for the Halictidae as a whole. Other largely tropical groups in the New World also lack close relatives elsewhere. These include various exomalopsine and nomadine genera, Tetrapediini, Centridini, Ctenioschelini, Euglossini, Rathymini, and certain subgenera of megachilids, xylocopines, etc. Some of these groups extend beyond the tropics both northward and southward, but all are to a major extent tropical. Some such taxa could have arisen from those that were in South America when it separated from Africa in Albian and Cenomanian times (Förster, 1978) (100 m.y. BP), but it is perhaps more likely that the ancestors of most of them arrived later and crossed the still narrow Atlantic, for there is no certainty that bees existed 100 m.y. BP, and the Atlantic remained narrow in the equatorial region for a long time.

The fact that meliponine distribution is best explained by assuming that these bees were in Gondwanaland before its break-up should be viewed with the understanding that it was the tropical parts of South America and Africa that separated last and were separated by narrow and probably island-filled seas. It would be more accurate to say that the Meliponinae were in Gondwanaland before its fragments became so isolated that the bees were unable to cross occasionally by rafting or other means. Presumably other bees would be more likely to cross such seas than Meliponinae. Lack of distributional evidence for such crossing by other groups of bees suggests that they were not yet present in the moist tropics when the continents separated.

There must also have been various taxa of bees that reached South America by island-hopping from North America during the Tertiary, evolved there, and became part of the Neotropical fauna. Any and perhaps all of the Neotropical groups listed above except the Meliponinae might fall in this category.

Several primarily Nearctic or Holarctic types extend in little modified condition into the Neotropics. Examples are *Halictus* (2 subgenera, *Halictus* s. str. to Trinidad and Colombia, *Seladonia* to central Brazil); *Calliopsis*, *Andrena*, and



*Heriades* (to Panama); *Anthophora* (to Argentina); and *Bombus* (to Tierra del Fuego). Such forms are far less numerous than the many Neotropical taxa that have a few species in the Sonoran or Chihuahuan deserts or other Nearctic areas. Thus in the recent interactions of the faunas, more tropical forms have adapted to seasonal warm north temperate areas than northern forms that have adapted to the tropics. The genera listed above probably entered South America since it was nearly or fully united with North America (union was about 5.7 m.y. BP).

The Neotropical bee fauna of North and Central America is much like that of tropical South America, although as indicated above, there is a small admixture of northern types such as *Andrena* and *Calliopsis*. Whatever tropical-adapted bees evolved in tropical North America and in Central America (insular or not) have become completely intermixed with those of South America, or belonged to the tropical South American groups to begin with, so that no distinction is now possible between tropical groups of South American and of North American origin.

Mountains, of course, have added greatly to the diversity of genera and species of the Neotropical fauna, but they are only part of the reason for the richness of this fauna compared to that of other tropical regions. Collecting experience and the meager data in Table 1 suggest that a given square mile of lowland forest contains many more species than an equivalent square mile in Africa or the Oriental region. A history of alternating wet and dry epochs (Haffer, 1969) with neither phase ever eliminating the other, may be responsible for this faunal richness. Likewise the much more extensive and diverse south temperate area, rich in bees, in South America than in Africa may have provided a source for tropical forms.

The *Antilles* contain only 18 tribal to familial taxa. *Nesomelecta* is considered distinct at the generic level and *Alayoapis* at the subgeneric level but otherwise all the forms are only specifically distinct from their continental relatives. Presumably, as for most other groups of organisms, the whole Antillean fauna must have arrived across the water. The fauna is depauperate Neotropical although there are a few taxa of Nearctic origin (*Nomia*, *Halictus*, *Heriades*). The greatest interest of the Antillean fauna from our standpoint is that it gives some idea of the island-hopping abilities of the various groups and of the faunas that must have inhabited the islands that existed in the seas between North and South America during much of the Tertiary, and that must have facilitated the faunal interchange between these continents.

The *southern Brazilian to Argentina region* has a large bee fauna. The southern part of the tropics in central and southern Brazil is progressively enriched as one goes southward by a mesic south temperate fauna, which also extends through Uruguay, and parts of Paraguay and Argentina. Group after group of Neotropical bees has additional genera or subgenera in this area. Thus this is the richest region, at least in the Neotropics, for Augochlorini, Panurginae, Exomalopsini, Nomadini, Eucerini, Xylocopini, etc. Since tropical forest fingers (e.g., along the coast, in the Paraná valley, and at Tucumán) extend into the savanna and grassland, many thoroughly tropical taxa also extend far south, with the result that the area of southern Brazil to Argentina has one of the richest mesic bee faunas in the world. Laroca's (1974) list is based on only three small areas (Table 1). To the south-

west the savanna and grassland part of southern Brazil–Argentina gradually becomes more xeric until in central Argentina there is desert vegetation similar in appearance to that of the Sonoran desert. Jörgensen's (1912) list of species of Mendoza shows something of the richness of this area.

The *Araucanian region* has a quite different bee fauna, lacking many of the typical Neotropical groups such as Meliponinae and Euglossinae, and having various unique and probably relict groups such as *Diphaglossa*, *Cadeguala*, *Corynura*, *Neofidelia*, *Manuelia*, and *Eucerinoda*. It is particularly rich in *Alloscirtetica* and Xeromelissinae, and has a larger diphaglossine fauna than any other area. It is also enriched by three genera which probably arrived by long distance dispersal from North America—*Penapis* (Dufoureae), *Orphana* and *Euherbstia* (Andreninae).

Both temperate South American areas considered above share in an abundance of Paracolletini. Except for Australia, this is the only region where this group is abundant. The Araucanian region also contains *Neofidelia*, the only fidelid known outside of southern Africa. The Gondwanaland source of such bees seems clear.

The moderate to high-altitude fauna of the Andes is probably mostly derived recently (since elevation of the Andes in late Tertiary) from faunas of southern South America, perhaps primarily from the Araucanian. Thus it includes *Alloscirtetica* and Paracolletini. It also includes characteristic genera of Augochlorini (e.g., *Andinaugochlora*), presumably derived from the fauna of southern Brazil to Argentina, or possibly directly from that of the wet tropics.

The *Nearctic region* shares many taxa with the *Palaearctic region*, and the two are quite legitimately joined to form the Holarctic. Certain genera (*Systropha*, *Rhophites*, *Panurgus*, *Dasypoda*, *Thyreus*, and others) are present in the Palaearctic but absent in the Nearctic. At the tribal and subfamilial levels only some small taxa (Apinae, Nomioidini, Pararhophitini, and Ammobatooidini) are present in the Palaearctic but not the Nearctic regions.

Dispersal across the North Pacific, and earlier in the Tertiary no doubt across the North Atlantic, is responsible for the similarity of the faunas of the two northern continents. To judge by the various Eurasian groups that reach North America only or chiefly in the west, most of the recent dispersal has been from Asia to North America and not in the reverse direction. Examples are *Chelostoma*, *Anthocopa*, *Dioxys*, *Melecta*, *Panurginus*, etc. Dispersal from North America to Eurasia, however, must have occurred, as illustrated by groups of Neotropical origin like *Nomada* and *Epeolus* that now range throughout the Holarctic area.

In contrast to the few Palaearctic groups that do not reach the Nearctic region, there are many major taxa in the Nearctic region that do not reach the Palaearctic. Nearly all have southern affinities. Some are clearly of Neotropical origin, such as *Caupolicana*, three genera of Augochlorini, *Protandrena*, various subgenera of *Megachile* and *Coelioxys*, *Exomalopsis* (2 subgenera), *Centris* (2 subgenera), one or more subgenera of *Nomada*, etc. Moreover, there are various groups found in both North and South America, more or less equally, which I believe to be of southern origin and which do not occur outside of the Western Hemisphere. Examples are Oxaeidae, *Agapostemon*, *Diadasia*, *Melitoma*, *Ancyloscelis*, and *Ptilo-*

*thrix*. Finally, a number of Neotropical taxa extend marginally into the Nearctic region, mostly in the Chihuahuan and Sonoran areas (for example, *Pseudaugochloropsis*, *Ptiloglossa*, *Temnosoma*, *Ptilomelissa*). The result is that the Nearctic region contains more tribes, subfamilies, and families of bees than the Palearctic or any other major faunal region (Table 3) and more genera and subgenera than any major fauna except the Neotropical.

The Palearctic fauna is also large and diverse (Table 3). Many groups are more abundant and diversified in the Palearctic region (including the Mediterranean) than elsewhere in the world. Examples are Bombini, *Halictus*, *Hoplitis*, Anthidiini, Dioxini, Anthophorini, and Melectini. A few predominantly African or Oriental groups appear to have remained in the southern Palearctic as the rest of the tropical fauna retreated with climatic deterioration, or extended north from Africa or the Orient into the southern Palearctic. Examples are *Nomia*, *Nomioides*, *Thrincohalictus*, *Exoneuridia*, *Ctenoplectra* (in the eastern Palearctic), *Amegilla*, *Thyreus*, and perhaps *Xylocopa* and *Ceratina*. Most of these forms probably arrived in the Palearctic in or since the Miocene when Africa and Eurasia were reunited. Except for *Exoneuridia* and *Thrincohalictus*, found only in Asia Minor, Palearctic species of all the genera listed are similar to African or Oriental species. Some groups probably entered the Palearctic from the Nearctic. Outstanding examples are the Exomalopsini-Ancylini, *Nomada*, and *Epeolus* (see section on DISJUNCTIONS), all of them ultimately Neotropical in origin.

The *Madrean area* (Californian plus the Sonoran and Chihuahuan deserts) is the climatic equivalent of the Mediterranean–Central Asiatic region, but appears to have had much better access to a tropical fauna than has the Old World equivalent. This applies especially to the Sonoran and Chihuahuan regions. In addition to the Nearctic taxa listed previously as originating in the Neotropics (*Caupolicana*, three genera of Augochlorini, etc.) and as widespread American (Oxaeidae, *Agapostemon*, etc.), all of which except *Augochlora* occur in the Madrean as well as the true Nearctic region, there are numerous Neotropical groups that occur in the Madrean, especially in the deserts, but do not or scarcely range into the mesic areas to the north of it. Such taxa are *Ptiloglossa*, *Zikanapis*, additional augochlorine genera, certain subgenera of *Centris*, Cteniochelini, and others. Most of the amphitropical genera listed in the section on DISJUNCTIONS are of south temperate origin and in the north are confined to or centered in the Madrean deserts. A noteworthy feature of the Nearctic region, and especially of the Madrean area, is the abundance of Panurginae, in sharp contrast to the Palearctic region.

The bee fauna of the Sonoran and Chihuahuan deserts may be roughly divided into two categories: first, those forms which have their seasonal flight in the spring and which collect pollen chiefly from the spring-flowering herbs, mostly annuals; and second, those forms which may or may not have their flight season in the spring and which collect pollen chiefly from typically Neotropical groups of plants, mostly trees and shrubs, that have penetrated the Sonoran region. Examples of such plants are *Larrea*, *Prosopis*, and *Cercidium*. The first group of bees consists of practically unmodified northern types (e.g., species of *Andrena*, *Anthophora*, *Synhalonia*, *Osmia*), the plants upon which they feed being likewise

northern and little modified except for shortening of the seasonal period of development as an adaptation to the xeric conditions. The second group of bees consists partly of southern types such as *Caupolicana*, *Protoxaea*, *Protepeolus*, *Martinapis*, *Centris*, and *Exomalopsis* (for details, see Michener, 1941), and partly of North American groups at least some of which are derived from northern groups of bees, e.g., *Ashmeadiella* and *Proteriades* derived from *Hoplitis* (= *Anthocopa*) and *Perdita*, a North American panurgine group of unknown derivation.

As in certain other xeric regions, there are in the Madrean area certain bees which appear to be relict forms. These include *Hesperapis*, *Megandrena*, and *Xeralictus*.

Although the arid part of the Palearctic region, i.e., the zone from the *Mediterranean basin to Central Asia* and beyond, contains an extremely rich fauna, it consists almost exclusively of the same tribal to familial groups that are in the mesic Palearctic. Some groups particularly richly represented in this xeric zone are Halictini, Anthidiini, osmiine Megachilini, Anthophorini, Dioxini, Melectini. Some groups largely limited to it are Ancylini, Pararhophitini, and *Eremaphanta*.

There are almost no taxa found in Africa and the Mediterranean basin but not also in more northern Eurasia, although such genera as *Nomia* and *Nomioides* nearly qualify as do certain Megachilinae. As indicated above in the account of the Palearctic, a few other genera that appear to be of southern origin extend well into the Palearctic region. Perhaps because the reservoir of tropical taxa is smaller in Africa than in the Neotropics, and because the major barriers (climatic, water, and montane) run east and west, the penetration of tropical types into the north temperate zone was much less in the Old World than in America.

#### SUMMARY

The bees arose from sphecoid wasps, probably in the upper Cretaceous, and perhaps in the arid parts of West Gondwanaland (Africa, South America). The earliest fossils, however, are from the late Eocene of Europe and these fossils include derived long-tongued bees (Apidae) as well as short-tongued bees of presumably more primitive families. The principal evolutionary achievement of the ancestral bees was their transfer from animal food to complete dependence on angiosperm floral resources. Bees have been much less successful than the angiosperms in adapting to humid conditions, and are still most abundant and diversified in some of the warm temperate arid regions of the world, especially those of North America and Eurasia. By contrast, bees, unlike many groups of organisms, are not unusually numerous or diverse in the tropics. The oriental tropics have a particularly poor fauna (89 genera and subgenera). Africa has a larger fauna (although perhaps not in the wet tropics) which was perhaps enlarged during dry periods that appear to have exterminated many organisms of the wet tropics. There are 175 genera and subgenera in tropical and austral Africa. The Neotropics with 315 genera and subgenera are relatively rich in bees, even in the wet tropics, perhaps because there has been a fluctuating pattern of both forest and savanna, and also because of continuity of the tropical region with the rich warm temperate fauna of South America. The comparable south

temperate fauna of Africa occupies a limited area and for this reason could not have been as rich a source of bees for the tropics; for the oriental tropics there is no comparable south temperate source except Australia which is isolated by ocean.

The diversity of faunas of major areas of the earth can often be related to interchanges among such areas. For example, the Nearctic faunal region (260 genera and subgenera) is richer than the Palearctic (243 genera and subgenera) largely because of the Neotropical elements in the Nearctic fauna. The main barriers between the Palearctic and nearby tropics (the Mediterranean Sea, the Saharan and Arabian deserts, the Himalayas, etc.) appear to have been more effective than the primarily climatic barriers between tropical North and Central America and temperate North America. Indeed, the Neotropics (presumably South America) appears to be the area of origin of some major groups of bees that have dispersed probably by island hopping to North America and thence spread widely. The best examples are *Nomada* and *Epeolus*, parasitic genera which were probably able to disperse extensively because of common, widespread, and previously unexploited hosts.

The distribution of most groups of bees can be explained on the basis of continents in approximately their present positions, without recourse to long-distance dispersal or great continental movements. No doubt this reflects the relatively recent origin and spread of most groups of bees. That dispersal across moderate ocean barriers can occur, however, in spite of fixed nest site preferences, is shown by the bees of islands. Thus New Zealand bees are derived from Australian groups, etc. Small bees and bees nesting in stems or wood seem more likely to reach islands than moderate sized or large ground nesting bees. The bee faunas of the Antilles and of certain of the Indonesian islands indicate that many bees can cross moderate ocean barriers and may use intervening islands in crossing broader oceans. Thus there was probably considerable faunal interchange via island stepping stones between continents such as North and South America, even when these continents were not connected.

While slow spread across continents and dispersal across currently moderate-sized barriers can account for most bee distributions, there are various, probably ancient groups for which distributional discontinuities can best be explained by continental movements or dispersal across oceans when they were relatively narrow. Examples are the paracolletines, almost entirely limited to temperate parts of the three southern continents, and the fideiids, limited to south and southwest Africa and Chile. The stingless honeybees (meliponines), limited to the tropics and southern subtropical regions, have several subgroups each occurring in two or three of the tropical land areas of the earth. Continental movements may well account for this distribution, especially since Africa and South America were connected or close together far longer in the equatorial region than in temperate areas.

The other disjunctions discussed are likely to be of much more recent origin. Certain amphitropical distributions almost certainly involve long distance dispersal, probably facilitated by dryer periods that reduced the distance between favorable habitats as compared to the present. Thus a considerable number of taxa of bees is found in warm temperate South America (mostly in deserts or

semi-deserts) and in the Sonoran and Chihuahuan deserts and sometimes elsewhere in North America, but not in the intervening tropics.

Another group of disjunctions involves the tropical and subtropical parts of Africa and the Orient. These areas could be nearly connected for bees living in grasslands or savanna by a somewhat moister climate across the Arabian peninsula, a likely condition at intervals in the past. Likewise, climatic change can account for various other disjunct distributions.

There remain several disjunctions for which no reasonably convincing explanation exists. All involve single taxa or groups, not groups of taxa, and therefore may result from isolated unlikely dispersal events. Given time, such unlikely events are likely to occur.

Many bees are restricted in pollen collecting to particular kinds of flowers. As one might expect, the distribution of such oligolectic bees is limited by the occurrence of host flowers. Some such bees have spread far beyond their original range when the plant has been dispersed by agriculture or horticulture. Most oligolectic bees, however, do not exist over the entire range of their floral host or do not occur with all populations of the host plant. It is clear that most plants, even when recognizable plant-bee coevolution has occurred, can exist and reproduce for long periods without their oligoleges, pollination from general pollinators such as polylectic bees sufficing. Indeed some oligoleges have nothing to do with pollination, but merely harvest pollen without transferring any to the stigmas, and thus are in effect parasitic.

The frequency of oligolecty appears to vary with climate, and is probably positively related to the number of kinds of bees simultaneously in flight in an area. Oligolecty is common, for example, in xeric North American areas, less common in mesic areas, and is rare in the tropics. Presumably it reduces competition among species, and would be especially important in areas like deserts with brief flowering seasons and many kinds of bees.

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